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Impacts of major watershed perturbations on aquatic ecosystems

Impacts des perturbations majeures des bassins versants sur les écosystèmes aquatiques

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Impacts of major watershed perturbations on aquatic ecosystems

Richard Carignan and Robert J. Steedman

Abstract: This Supplement presents data syntheses and new evidence from temperate (primarily boreal) North American studies of aquatic ecosystem response to episodic watershed deforestation and acid rain. These studies confirm the dominant role of the watershed in modulating aquatic response to terrestrial disturbance and quantify important regional differences related to physiography, vegetation, and drainage patterns. Comparisons of watershed disturbance by wildfire and logging revealed both similarities and differences in aquatic impact and underscore the need for ongoing regional evaluation of forest management models based on simulation of natural disturbance patterns. General quantitative impact models are now available but tend to be regional in scope and relevant primarily to water yield and water quality, rather than to habitat and biota.

Résumé : Ce supplément présente de nouveaux résultats et de nouvelles synthèses sur la réponse des écosystèmes aquatiques aux perturbations telles l'acidification et la perte de couverture forestière par la coupe forestière et les feux de forêt. Ces études confirment le rôle modulateur du bassin versant et mettent en évidence le caractère régional des effets selon la physiographie, la végétation et le drainage des bassins versants. La comparaison des effets produits par les feux et la coupe montre que leurs effets peuvent être semblables ou différents, selon les indicateurs choisis. Les impacts différents du feu et de la coupe révèlent que les modèles d'aménagement forestier basés sur les régimes de perturbations naturelles sont imparfaits et qu'ils doivent être évalués régionalement. Les modèles d'impact disponibles ont un caractère régional et visent surtout la prédiction de l'écoulement et de la qualité des eaux; ces modèles tendent à négliger les aspects liés à la qualité de l'habitat et à la réponse des communautés biologiques.

There are two key science questions underlying contemporary concerns about sustainability of healthy waters in forested landscapes: (*i*) has human activity threatened the ability of forested watersheds to produce clean water and support diverse, productive aquatic biota? and (*ii*) will new stresses exacerbate or counteract existing ones? Research to answer these questions must examine similarities and differences between historical and contemporary mechanisms, patterns, and intensity of watershed disturbance. This Supplement presents data syntheses and new evidence to update our understanding of lake and stream response to a very important suite of watershed disturbances: acid rain and deforestation by clearcutting and wildfire.

The watershed (also referred to by some authors as a catchment, basin, or drainage) is not the only part of the world that influences runoff, water quality, and aquatic biota in forested landscapes but it is a very important one. Watersheds have long provided a useful model for hydrologists and geochemists studying effects of forest disturbance on water yield and solute export. However, quantification of impacts on aquatic habitat and biota has lagged behind that of physical and chemical impacts. This has been due in part to the complex linkages between terrestrial and aquatic phenomena at spatial and temporal scales relevant to watershed processes. Such processes include runoff generation and modulation at small to large spatial scales, movement of dissolved and suspended material from forests and soils into surface and subsurface water, and the influence of deforestation and geomorphic disturbance. Additional complexity arises from vegetation and soil disturbance associated with climate change and with the long-range atmospheric transport and deposition of acid-generating substances and contaminants (Schindler 1998).

Water quality and aquatic biota are strongly influenced by the condition and disturbance regimes of catchment soils and vegetation. Historical mechanisms of forest and soil disturbance in temperate North America included wildfire, windthrow, defoliation by insects, and climate change. Human activity in recent decades has added wildfire suppression, forestry, acid deposition, and stratospheric ozone depletion, as well as urban development and agriculture. The spatial scale and pattern of forest disturbance is important because most aquatic impacts are driven by altered hydrologic cycles and therefore are related to the extent of catchment disturbance. Wildfire and forestry are both associated with temporary local deforestation but have different mechanisms and may exhibit important differences in spatial extent and frequency of occurrence and in their impact on water quality.

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Disturbances of atmospheric origin (e.g., acid deposition, ultraviolet radiation, and greenhouse gases) are associated with widespread changes to forest vegetation and soils and may also lead to long-term deforestation. Empirical and theoretical models of aquatic response to wildfire and forestry will differ from those required for impacts of atmospheric origin.

Forest management practices are shifting towards natural disturbance-based models (Hunter 1993). These models propose that fire and logging have similar impacts on ecosystems and that forest exploitation patterns emulating fire should preserve ecosystem integrity. These important assumptions remain largely unverified, however, for both terrestrial and aquatic ecosystems. Potential synergisms between wildfire, logging, acid rain, and climate change are also largely unexplored.

Three general themes were addressed by the contributions to this Supplement and are briefly summarised below.

Acid rain

In response to the Canada–U.S. Air Quality Agreement, both countries have reduced SO_2 emissions during the last decade and further reductions are projected between 2000 and 2010. Jeffries et al. (2000) use a modelling approach to assess the ecological adequacy of these reductions by evaluating the change in lake pH expected to occur in southeastern Canada. They conclude that after full implementation of projected emission controls, between 5% and 24% of lakes in the six regions considered will still remain chemically damaged.

Streams: water yield, quality, and temperature

Although many studies have described the effects of forest harvesting on water yield and water quality in streams, long-term responses have seldom been examined. Martin et al. (2000) provide 14- and 27-year-long time series describing the impacts of harvesting on the hydrology and nutrients dynamics of two northern hardwood streams (White Mountains, New Hampshire). In these watersheds, water yield, peak flow, and stream chemistry return close to preharvest conditions within 3 to 6 years. In comparison, high runoff is expected to persist decades after forest clearance in the boreal forests of eastern Canada (Plamondon 1993). Nevertheless, Martin et al. (2000) further observe that significant disruptions in Ca^{2+}, K^+, and NO_3^- export still persist 27 years after harvesting. For poorly known reasons, the large increase in NO_3^- export observed by Martin et al. contrasts with the results of Lamontagne et al. (2000), who found no, or very limited, NO_3^- loading to boreal lakes following the removal of a large proportion of the forest on their watersheds. Such results are typical of the response variability found in other watersheds and illustrate the incomplete state of our knowledge of the effects of harvesting on the nitrogen cycle (Vitousek 1981). Another informative time series on the long-term effects of riparian vegetation removal by clearcutting and scouring by debris flow is presented in Johnson and Jones (2000). The pronounced increases in stream temperature measured after these perturbations returned to pre-impact levels after 15 years.

The suite of perturbations presently affecting our surface waters does not operate at comparable spatial and temporal scales. While the actions of climate change and acid rain are global or regional, other major watershed disruptions such as wildfires and harvesting are spatially fragmented and produce maximum impacts at the local scale (tens to hundreds of hectares). Scaling-up the effects of local perturbations on the hydrological and biogeochemical cycles may not be trivial, as shown by Buttle and Metcalfe (2000). These authors examined relationships between recent forest disturbance and streamflow responses in large (400 – 12 000 km^2) watersheds of northeastern Ontario. They concluded that although watershed deforestation (5–25% by area) was not associated with significant impacts on annual yield or peak flow magnitude or timing, there were increases in summertime low flows.

Disruptions of biogeochemical cycles following the loss of forest cover can be caused by several factors including severe alterations of major nutrient sinks and sources, increases in soil temperature and humidity, changes in soil structure caused by logging equipment, and hydrological flushing of nutrients and coloured dissolved organic carbon (DOC) from surficial organic soil layers into surface waters, as the result of elevated water tables. Evans et al. (2000) illustrate the potential importance of hydrological flushing in the boreal plain of Alberta, where rises of the groundwater table was associated to large increases in soil water dissolved P. Although P is geochemically immobile in the mineral layers of acidic podzols, the same mechanism is invoked in Carignan et al. (2000) to explain increases in lake water P and DOC following harvesting.

Lakes: water quality, chemical budgets, and physical and biotic effects

Using before-and-after comparative and paleolimnological approaches, 11 contributions to this Supplement examine the effects of watershed deforestation by clearcutting and (or) wildfire on the chemical, physical, and biological properties of lakes. Lake response to deforestation should resemble that of streams but may be delayed and reduced because of dilution of runoff in lake volume. Some apparently contrasting results obtained by different authors for key limnological properties (DOC, colour, P, N) highlight the importance of lake and watershed characteristics in determining the effects of harvesting on water quality. Steedman (2000) found only modest changes in DOC, nutrients, and major ion concentrations following clearcutting around deep headwater lakes of the Coldwater Lakes Experimental Watersheds in northwestern Ontario. Scully et al. (2000) found no paleolimnological evidence for increased flux of nutrients and organic matter following clearcutting around a Michigan lake. On the other hand, Carignan et al. (2000) reported that concentrations of most dissolved constituents were substantially higher in central Québec lakes simultaneously impacted by wildfire or clearcutting, as compared with similar reference lakes. These impacts were directly proportional to the surface area harvested divided by lake size, measured as volume or surface area. Such different results appear entirely attributable to the widely different morphometries, drainage ratios, and water renewal times of the lakes described in the three studies. The lakes studied by Steedman (2000) and Scully et al. (2000) have small (2–3) drainage ratios compared with those (2–15) studied by Carignan et al. (2000). The empirical

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models proposed in Carignan et al. (2000) for DOC, light penetration, total P, and major ions predict only weak effects at low drainage ratios and are thus consistent with the observations of Steedman (2000) and Scully et al. (2000).

The impacts of forest removal by wildfire and harvesting are not identical. Although both perturbations caused similar exports of K, total phosphorus, and nitrogen to central Québec lakes (Lamontagne et al. 2000), harvesting produced more DOC compared to fire, and fire caused a large increase in NO_3^- export compared to harvesting. Nitrogen was released mainly as organic forms by harvesting and mainly as inorganic forms by fire. Using a paleolimnological approach, Enache and Prairie (2000) confirmed the observations of Carignan et al. (2000) and inferred significant (up to two-fold) increases in total P concentration but no change in DOC and pH following fire in the watershed of a humic kettle lake in Abitibi (drainage ratio = 20). In contrast, McEachern et al. (2000) attributed high DOC concentrations to wildfire in subarctic Alberta, where black spruce forest are underlain by thick organic soils and discontinuous permafrost. Furthermore, McEachern et al. (2000) did not detect significant enrichments in base cations in lakes impacted by fire. Such different responses to watershed perturbations illustrate the danger of extrapolating effects observed in one particular region to other areas where different physiographic and edaphic conditions may prevail.

On the Canadian Shield and in the Hudson's Bay lowlands, decades of high anthropogenic mercury deposition from the atmosphere and favorable biogeochemical conditions for its methylation have created a widespread toxic methyl mercury (MeHg) contamination problem in game fish. Results by Garcia and Carignan (1999, 2000) on Hg concentrations in zooplankton and northern pike (*Esox lucius*) collected in the Québec lakes described in Carignan et al. (2000) suggest that forest harvesting further accentuates the problem, presumably through increased DOC loading to impacted lakes. If confirmed by further studies, this effect should be taken into consideration in future harvesting practices.

Three studies describe the propagation along the food chain of the nutrient pulses generated in lakes by fire and, to a lesser extent, by harvesting. Planas et al. (2000) monitored the composition and biomass of pelagic and benthic algae in the same lakes described by Carignan et al. (2000). In addition to significant differences in species composition between treatments, they observed two- to three-fold higher concentrations of chlorophyll and biomass in perturbed lakes compared with reference lakes. For a given degree of watershed perturbation, lakes impacted by fire had more pelagic chlorophyll than lakes impacted by harvesting. In addition, lakes impacted by fire produced more pelagic chlorophyll per unit total P than lakes impacted by harvesting, which indicates that the biological availability P forms exported from burnt and clearcut watersheds may differ. The high nutrient and algal concentrations observed in perturbed lakes produced relatively modest differences in zooplankton abundance and composition (Patoine et al. 2000). Significant differences were detectable only during the first 2 years following perturbation and were more pronounced in lakes impacted by fire than in those impacted by harvesting.

Higher up in the food chain, St-Onge and Magnan (2000) did not detect any difference in catch per unit effort of dominant fish species or in the growth rate of yellow perch (*Perca flavescens*). These authors did observe, however, abnormally low proportions of small individuals and possible recruitment failures in the populations of yellow perch and white sucker (*Catastomus commersoni*) found in lakes impacted by harvesting and fire. These studies suggest that the effects of watershed perturbations by fire and harvesting may become increasingly subtler at higher trophic levels, at least in terms of biomass. It is also possible that at higher trophic levels, between-lake variability in species composition and abundance renders inappropriate the short-term comparative approach used in the Québec lakes to quantify the effects of perturbations by fire and harvesting.

Removal of the forest cover may increase wind exposure and decrease water clarity in lakes. These effects may in turn influence fish habitat by changing thermal stratification, the mixing regime, and hypolimnetic dissolved oxygen concentrations. Two studies, by Steedman and Kushneriuk (2000) and Scully et al. (2000), address these questions. Steedman and Kushneriuk (2000) reported that clearcut logging without buffer strips around 30- to 40-ha dimictic lakes increased midlake wind speed by 5% or less, with no measurable changes in circulation efficiency, duration of stratification, and lake trout (*Salvelinus namaycush*) habitat volume. Scully et al. (2000) used paleolimnological methods in a small (8 ha) twin-basin humic-stained lake to show that clearcut logging followed by wildfire coincided with a long (75+ years) period of increased circulation efficiency, leading to a reduction of deepwater anoxia and the elimination of anaerobic photosynthetic bacteria. These studies suggest that increased wind stress effects following deforestation vanish rapidly with increasing lake size and may occur only when the riparian vegetation has been lost. It should be noted, however, that both studies were conducted on lakes that have a small drainage ratio, where little increase in coloured DOC is expected after harvesting. Lakes with larger drainage ratios are expected to receive more coloured DOC after harvesting. In such lakes, decreased light penetration may exert a stronger influence than increased wind stress on mixing regimes (Schindler et al. 1997).

Some effects of harvesting on fish populations may be quite indirect but potentially more damageable than the changes in habitat quality presumed to arise in streams or lakes following harvesting. An original experiment by Gunn and Sein (2000) suggests that although that lake trout can tolerate substantial losses in spawning habitat by siltation, increased fishing pressure following the construction of forest access roads can result in severe overexploitation of lake trout populations in small lakes.

Most conceptual and quantitative impact models presented in this Supplement are directly applicable to the preservation of aquatic resources. These models are by no means complete or definitive, however. They tend to remain regional in scope and to address primarily water yield and water quality issues, rather than habitat and biota. The lakewater quality models found in the Supplement remain essentially empirical. As our knowledge of the in-lake reactivity of DOC, nutrients, and contaminants increases, water quality models will no doubt improve by replacing them by more mechanistic models linking hydrology to export coefficients from wa-

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tersheds and to in-lake reaction rates. The cumulative effects of other extensive watershed disturbances such as ore, oil, and gas exploration are still largely undescribed, even if these activities create access roads and locally clear trees at rates that are comparable with commercial logging operations. We hope that the ideas and results collated in this volume will stimulate further research on the impacts of watershed perturbations on aquatic ecosystems.

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Boreal forest disturbance and streamflow response, northeastern Ontario

J.M. Buttle and R.A. Metcalfe

Abstract: The effects of forest disturbance on streamflow from small (<10 km^2) basins have been well documented; however, implications of such disturbance for streamflow from relatively large rivers in the Canadian boreal forest are unclear. Landsat imagery was used to determine changes in the type, amount, and location of forest disturbance in northeastern Ontario between 1985 and 1990. These were compared with streamflow responses from medium- and large-scale basins in the region. Harvesting dominated forest disturbance, and total disturbance as of 1990 ranged from 25% of basin area in the northwest part of the region to 5% in the southeast. There was limited streamflow response to land cover changes, with no definitive changes in water year runoff or peak flow magnitude and timing. This likely reflects the ability of relatively large basins to buffer the hydrologic impacts of the small degree of recent forest disturbance, combined with the influence of climatic variability on temporal trends in basin streamflow. However, disturbance was associated with increases in moderate and low flows from medium and large basins, respectively, which occurred largely during summer months.

Résumé : Les effets des perturbations de la forêt sur l'écoulement dans les petits bassins (<10 km^2) sont bien documentés, mais les incidences de ces perturbations sur le débit de cours d'eau relativement grands dans la forêt boréale canadienne ne sont pas clairs. Nous avons eu recours à l'imagerie Landsat pour déterminer les changements dans le type, l'importance et la localisation des perturbations de la forêt dans le nord-ouest de l'Ontario entre 1985 et 1990. Nous avons comparé ces éléments aux réactions dans l'écoulement de bassins d'échelle moyenne à grande dans la région. C'est l'exploitation forestière qui dominait les perturbations, et la perturbation totale en 1990 allait de 25% de la superficie du bassin dans la zone nord-ouest à 5% dans le sud-est. La réaction de l'écoulement au changement dans la couverture du sol était limitée, et aucun changement définitif n'a été noté dans le volume d'écoulement annuel ni dans l'ampleur et le calendrier des pics de débit. Cela s'explique vraisemblablement par l'aptitude des bassins relativement grands à compenser les impacts hydrologiques d'un faible degré de perturbation récente de la forêt, combinée à l'influence de la variabilité climatique sur les tendances temporelles du débit des bassins. Toutefois, la perturbation était associée à des hausses des écoulements modérés et faibles des bassins de taille moyenne et grande, respectivement, qui se produisaient essentiellement pendant les mois d'été.

[Traduit par la Rédaction]

Introduction

The boreal forest is the dominant forest type in Canada, covering ~3 million km^2 (Zoltai et al. 1988). Frequency and intensity of disturbance of forest cover by fire are increasing in some parts of the boreal region (e.g., northwestern Ontario; Stocks and Street 1983) while decreasing elsewhere (e.g., northwestern Quebec; Dansereau and Bergeron 1993). Nevertheless, there appears to be a general increase in the rate and magnitude of disturbance by harvesting in many parts of the boreal forest (Schindler 1998). Research in the boreal forest, and to a greater extent in other forest types, has shown that forest disturbance can affect a range of aspects of basin streamflow. Total runoff (water yield) generally increases with forest disturbance (Bosch and Hewlett 1982; Sahin and Hall 1996), with reduced interception and transpiration leading to greater streamflows. Total runoff increases roughly in proportion to the fraction of basin basal area harvested (Keenan and Kimmins 1993), although the exact relationship varies between regions and forest type (Sahin and Hall 1996; Stednick 1996). The literature provides "mixed messages about peak flow responses" (Thomas and Megahan 1998, p. 3402) to forest disturbance, with reports of increases (Verry et al. 1983; Jones and Grant 1996), increases for only small peak flows (Thomas and Megahan 1998), decreases (Harr and McCorisin 1979), and no significant changes (Thomas and Megahan 1998) following harvesting. Variations in peak flow response to disturbance likely reflect intersite differences in such factors as the dominant runoff-generating process(es), climate, geology, topography, vegetation cover, soils, and the harvesting strategy employed. There is greater consensus that summer rainfalls that do not generate a streamflow response in forested basins may produce small to moderate flows in disturbed basins (Pomeroy et al. 1997). This is due to greater soil water storage resulting from reduced evaporation (Elliot et al. 1997), combined with soil compaction and enhanced potential for soil saturation and overland flow. Disturbance may also alter

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Table 1. Physical properties of the study basins.

Water Survey of Canada station No. (basin code)	Station name	Area (km^2)	Lowest elevation (m asl)	Highest elevation (m asl)	Relief ratio[a]	Physiographic units (fraction of basin area)		
						Till plain	Lacustrine plain	Upland
04LK001 (M1)	Mattawishkwia River at Hearst	1 140	230	334	0.001 30	0.42	0.58	0.00
04LJ001 (L1)	Missinaibi River at Mattice	8 940	224	512	0.001 52	0.22	0.54	0.25
04LF001 (L2)	Kapuskasing River at Kapuskasing	6 760	201	500	0.001 39	0.31	0.19	0.50
04LD001 (L3)	Groundhog River at Fauquier	11 900	275	507	0.002 13	0.10	0.36	0.54
04LB001 (L4)	Mattagami River at Smooth Rock Falls	10 000	215	451	0.000 99	0.15	0.30	0.55
04MD004 (M2)	Porcupine River at Hoyle	401	271	310	0.001 26	0.06	0.94	0.00

[a]Relief ratio = H/L, where H is difference between the highest and lowest points in the basin and L is the horizontal distance along the longest dimension of the basin parallel to the principal drainage line.

the timing of peak flows. Snow cover in disturbed areas ablates before appreciable melt in forest stands. This produces several small peak flows, rather than a large peak flow from basin-wide snowmelt (Verry et al. 1983). The date of the annual peak flow may also be advanced (Cheng 1989). There appears to be a general increase in low flows following disturbance due to wetting-up of the basin because of reductions in rain and snow interception, sublimation, and evaporation (e.g., Hartman and Scrivener 1990; Dubé et al. 1995; Prevost et al. 1999).

Most studies of the hydrological impacts of forest disturbance have been conducted at small scales (<1 to 10 km^2; Bosch and Hewlett 1982; Sachs et al. 1998), and the cumulative impacts of these local disturbances on streamflow at the medium- (~100 km^2) or large-basin (~1000 km^2) scales are unclear (Cheng 1989; Sahin and Hall 1996). Keenan and Kimmins (1993) contended that if only a small proportion of first-order basins experience increased streamflow due to harvesting, these effects are much reduced in second- and third-order basins and are often undetectable in fourth- and fifth-order streams. Cheng (1989) found significant changes in streamflow from forested basins >10 km^2 in area, provided a sufficient portion of the basin was harvested. Coats and Miller (1981) noted that the cumulative effects of concentrated harvesting in large basins can lead to larger impacts on major rivers relative to those in smaller basins. The validity of predicting the cumulative impact of forest disturbance on large river systems by simply scaling up experimental results from small basins has been questioned (Cheng 1989), based on such concerns as uncertainties about flood arrival times from different tributaries and the inverse relationship between the frequency of runoff events of a given magnitude and basin size (Coats and Miller 1981).

Despite the uncertainty regarding the cumulative effects of forest disturbance on the hydrology of medium- and large-scale basins, information is needed on the streamflow response to disturbance at these spatial scales in order to address the associated implications for such issues as aquatic ecology, water supply, and generation of hydroelectricity. This paper examines (*i*) recent forest disturbance patterns in the boreal forest of northeastern Ontario and (*ii*) streamflow responses from medium- and large-scale basins in the region to this disturbance.

Materials and methods

Study area

The study basins are the southwestern and southern tributaries of the Moose River basin, which drains northeastern Ontario and part of western Quebec northward to James Bay (Fig. 1; Table 1). They were selected to examine the effects of forest disturbance on streamflow at the medium- (04LK001 and 04MD004, henceforth referred to as M1 and M2) and large-basin (04LJ001, 04LF001, 04LD001, and 04LB001, henceforth referred to as L1, L2, L3, and L4) scales. The basins overlie Precambrian Shield igneous and metamorphic rocks (Superior Province) of Neo- to Meso-archean age (2.5–3.4 Ga) and have limited relief and low gradients. Lower portions of the medium basins overlie till plain, while higher elevations are on lacustrine plain. Stream headwaters in the large basins originate on Shield uplands and traverse the lacustrine plain to outlets on the till plain.

Upland portions of the basins are largely mantled by well-drained orthic humoferric podzols with a stony–rocky phase, while lower elevations are dominated by well-drained gray luvisols and poorly drained mesisols and orthic gleysols (Clayton et al. 1977*a*, 1977*b*). Forests (including treed wetlands) cover from 79 (M2) to 89% (L2) of basin area. Forests in upland areas are dominated by black and white spruce, along with balsam fir, jack pine, white birch, and trembling aspen, while forested wetlands contain tamarack and black spruce. Wetlands, cutovers, lakes, and agricultural, mining, and urban areas comprise a small proportion of each basin's surface cover (Buttle et al. 1998).

The basins are in the Dfb modified Köppen climate zone: continental cool summer boreal forest climate, adequate precipitation throughout the year for vegetative growth, 4 or more months with mean temperatures >10°C, and mean temperatures in the coldest month lower than −3°C (Royal Commission on the Northern Environment 1985). There is a general increase in water year (WY: 1 October of one year to 30 September of the next) precipitation from northwest to southeast across the study area, while the fraction of WY precipitation contributed by snowfall decreases along the same gradient (Table 2). Mean WY runoff ranges from ~350 to ~450 mm, while mean WY evaporation (residual of simplified water balance) ranges from ~410 to ~453 mm. Flow from L2, L3, and L4 is regulated as a result of hydroelectric dam operation. Regulation has reduced peak runoffs relative to unregulated basins, with the greatest impact on flows equaled or exceeded <5% of the time (Buttle et al. 1998).

Disturbance

Disturbance was assessed using two classified Landsat images

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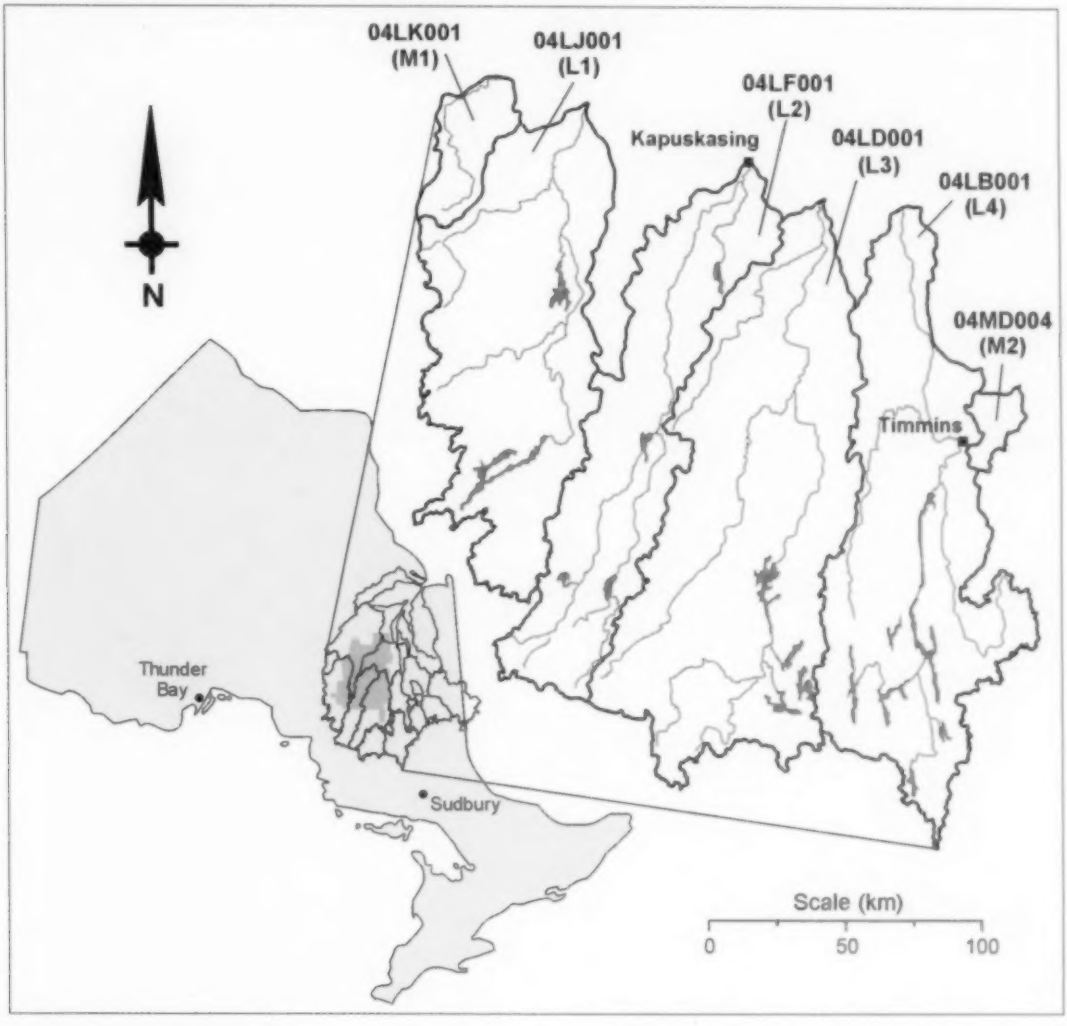
Fig. 1. Location of the study basins. The heavily stippled area on the Ontario map indicates the area in the west-central portion of the Moose River basin for which estimated harvested area between 1985 and 1990 obtained from Landsat imagery was compared with actual harvested area obtained from Ontario Ministry of Natural Resources records.



from the Ontario Ministry of Natural Resources. The first was a multispectral scanner (MSS) image based on summer scenes at 100-m resolution. Scenes were taken on various dates in 1984 and 1985 to achieve cloud-free coverage of the Moose River basin. Classification employed supervised training and a maximum likelihood classifier on four bands of MSS data (White and Ellis 1987). The second image was a thematic mapper (TM) image based on summer scenes taken at 25-m resolution in 1990 and 1991. The TM classification was resampled to match the 100-m resolution of the MSS classification. Classification employed supervised training and a maximum likelihood classifier on seven bands of TM data (Spectranalysis Inc. 1997). Disturbance was classified as "cutovers" or "burns" in the MSS image and as "recent cutovers" (<10 years old), "recent burns" (<10 years old), and "old burns and cutovers" (up to 50 years old) in the TM image (Fig. 2).

To relate forest disturbance to basin streamflow, the MSS and TM images were assumed to represent conditions as of 1985 and 1990, respectively. The 1985 classification does not indicate the age of cutovers or burns, such that their state of regeneration when the imagery was taken is unknown. Therefore, cutover and burn classes on the 1985 image represent the upper bound of disturbed area, since some areas may have been in an advanced state of regeneration and may have been similar hydrologically to mature forest stands (cf. Pomeroy et al. 1997). There were no major fires in the basins during the 1976–1996 period according to data from the Fire Science and Technology Branch, Ontario Ministry of Natural Resources, and areas classified in the 1985 image as burns and in the 1990 image as recent burns represented <0.01% of the combined basin areas. Therefore, burns and recent burns were not included in the analyses. Some 1985 cutovers were classified as recent cutovers in the 1990 image. These areas would not have been harvested between 1985 and 1990 and were subtracted from recent cutovers in the 1990 image to estimate the extent of harvesting between 1985 and 1990. The accuracy of this assumption was assessed by comparing the estimated extent of harvesting (square kilometres) between 1985 and 1990 in an area in the west-central

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Fig. 2. Disturbed areas in the study basins based on the 1985 and 1990 images. Burns (1985 image) and recent burns (1990 image) comprised a minor portion of the basin areas and were not plotted.

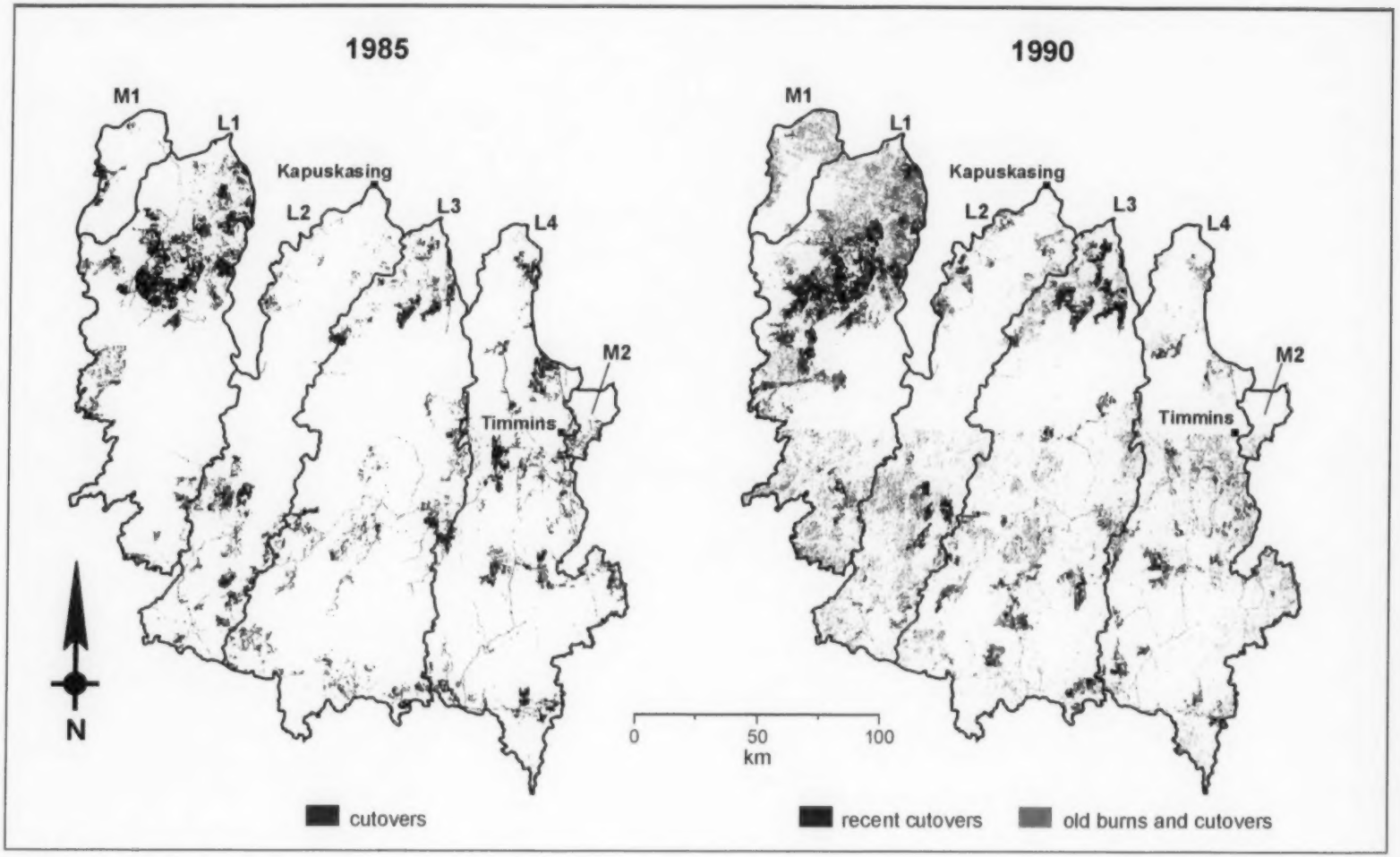

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Table 2. Water balance summary statistics for study basins (mean ± 1 SD) (from Buttle et al. 1998).

Basin	Water Survey of Canada station name	Period of record	WY precipitation (mm)	WY snowfall/WY precipitation	WY runoff (mm)	*R:P* ratio[a]	WY evaporation (mm)
M1	Mattawishkwia River at Hearst	1986–1993	844±76	0.35±0.06	417±103	0.49±0.10	427±75
L1	Missinaibi River at Mattice	1920–1995	811±100	0.35±0.04	366±85	0.45±0.09	446±91
L2	Kapuskasing River at Kapuskasing	1920–1995	807±98	0.33±0.04	360±78	0.45±0.08	446±89
L3	Groundhog River at Fauquier	1920–1995	802±97	0.33±0.04	382±80	0.48±0.09	417±87
L4	Mattagami River at Smooth Rock Falls	1920–1995	813±102	0.33±0.04	351±74	0.43±0.09	462±96
M2	Porcupine River at Hoyle	1977–1993	895±77	0.31±0.04	442±68	0.49±0.06	453±63

[a]WY runoff ÷ WY precipitation.

Table 3. Disturbance characteristics of the study basins.

	M1			L1			L2			L3			L4			M2		
	1985	1990		1985	1990		1985	1990		1985	1990		1985	1990		1985	1990	
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Area (km^2)	49	7	209	922	603	1654	345	220	615	640	526	761	788	277	582	34	1	19
% of basin	4.3	0.6	18.3	10.7	6.7	18.5	5.0	3.3	9.1	5.1	4.4	6.4	8.1	2.8	5.8	8.5	0.2	4.7
Largest patch index (%)[a]	2.0	0.3	4.8	1.0	6.8	3.5	0.5	0.4	0.2	0.4	0.6	0.2	0.9	0.4	0.2	2.5	0.2	0.9
No. of patches	56	66	1184	810	4203	10 013	565	2000	5368	1031	3884	7263	810	2696	6106	59	20	202
Patch density ($no.\cdot km^{-2}$)	0.05	0.06	1.04	0.09	0.49	1.16	0.08	0.29	0.78	0.08	0.31	0.58	0.08	0.28	0.62	0.15	0.05	0.51
Mean patch size (km^2)	0.92	0.12	0.19	1.02	0.25	0.14	0.64	0.15	0.10	0.64	0.19	0.08	1.02	0.16	0.07	0.58	0.08	0.09
CVN	0.141	0.045	1.140	0.352	0.510	0.989	0.204	0.238	0.608	0.213	0.288	0.391	0.278	0.257	0.393	0.421	0.025	0.359

Note: 1, cutovers; 2, areas estimated to have been harvested between 1985 and 1990; 3, old burns and cutovers on the 1990 TM image plus cutovers on the 1985 MSS image classed as recent cutovers on the 1990 TM image.

[a]Percentage of basin area occupied by the largest patch.

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portion of the Moose River basin (Fig. 1) with the observed extent of harvesting between 1985 and 1990 in the same area based on Ontario Ministry of Natural Resources data. Cells subtracted from the 1990 recent cutovers were added to the old burns and cutovers from the 1990 TM image, and total disturbance as of 1990 within each basin was estimated as the sum of harvesting between 1985 and 1990 plus the augmented old burns and cutovers.

The potential effect of forest disturbance on basin hydrology depends on several factors in addition to the amount of disturbance relative to basin area. These include the nature of the surface on which disturbance occurred, the proximity of disturbed areas to the drainage network (Thomas and Megahan 1998), and the pattern of disturbance within the landscape (i.e., fragmented or clumped). Relative differences in infiltration properties between surface types could lead to variations in runoff response to the same amount of harvesting on each surface type. Therefore, the extent of harvesting between 1985 and 1990 on each of the major physiographic units in the basins (Table 1) was determined. Harvesting of wetlands generally increases water table levels (Dubé et al. 1995), and the consequent expansion of saturated areas may enhance streamflow generation and increase peak flows and total runoff. However, the extent of disturbance on wetland surfaces was not assessed, since these localized impacts were felt to be undetectable at the scale of basins studied here.

In order to assess disturbance patterns with respect to the drainage network, the Euclidean distance from each cell in a basin to the nearest water body (major stream or lake) in the basin was calculated from 1:250 000 digital National Topographic Series drainage network coverage. Cumulative total basin area and total area of forest disturbance with increasing distance from the drainage network were then determined for each basin. Using Euclidean distance instead of flow pathways will tend to underestimate the true distance of cells to the drainage network. A better estimate would be obtained using drainage flowpaths, the accuracy of which is a function of the basin digital topographic model used to estimate flowpath length. However, the size of the study area and resolution of the available provincial digital topographic model (1 × 1 km) made derivation of flow pathways impractical.

Disturbance patterns were analysed for the 1985 and 1990 images using indices at the patch and landscape scale. Each disturbance type was analysed separately within each basin. Cells classified as one of the disturbance types were grouped into contiguous patches if they contained the same attribute and touched in any of the eight possible cardinal directions. At the landscape scale, the contiguity of disturbed patches was assessed using the center versus neighbors (CVN) index (Murphy 1985). CVN was calculated on a cell-by-cell basis using a 3 × 3 kernel, and the mean was determined for each basin. The CVN is simply the number of cells different from the center cell in the kernel. Index values range from 0 (all cells of the same class) to 8 (center cell different from all neighbors), representing a decreasing degree of contiguity and an increasing degree of landscape fragmentation.

Streamflow

The paired-basin approach (with two or more basins of similar geology, topography, soil cover, and climate) offers the best means of assessing streamflow response to land-use change (Bosch and Hewlett 1982) where one basin serves as a control, while land cover on the other basin(s) is modified. However, absence of nearby control basins that did not experience land cover changes between 1985 and 1990 necessitated a "quasi-paired-basin approach" (Buttle 1996), with partial control at a given scale provided by the basin with the least forest disturbance during the period (i.e., M2 was the partial control for M1, and L4 was the partial control for L1, L2, and L3).

Water Survey of Canada daily mean discharges (cubic metres per second) for all basins for the period of record (Table 2) were converted to daily runoff (millimetres oer day) to permit comparison between basins of different sizes. WY runoff was calculated for each basin for WYs with complete records. Daily total precipitation and snowfall data were obtained from all Atmospheric Environment Service climate stations operating in and around the basins for the period 1920–1996. WY total precipitation and total snowfall were calculated for each station by summing October–September monthly totals. These point data were then used to compute spatially averaged annual total precipitation and snowfall values for each basin for any WYs with complete runoff records, as described in Buttle et al. (1998). WY runoff was divided by total precipitation to obtain the WY runoff ratio.

Double-mass curves (DMCs) of cumulative runoff from M1 versus M2 and from L1, L2, and L3 versus L4 were constructed. Linear regression equations were fit to the medium-basin DMC. Missing streamflow data for L3 required division of the runoff record into two periods: 1920–1966 and 1970–1993. Linear regression equations were fit to the large-basin DMCs for each of the following periods: 1920–1966, 1970–1993, 1970–1984, and 1985–1993. The latter period approximated the time interval during which forest disturbance within the basins was assessed. DMCs of cumulative precipitation for M1 versus M2 and for L1, L2, and L3 versus L4 were also constructed for the same time periods used for the runoff DMCs.

Flow regulation of L2, L3, and L4 meant that the peak and low flow response of only the unregulated basins (M1, M2, and L1) was examined for the period of concurrent flow record (1986–1993). Partial duration series were constructed, consisting of all peak flows equal to or greater than the smallest annual maximum flow for the basin for the 1986–1993 period. Each peak flow was categorized according to the type of generating event (snowmelt versus rainfall versus rain-on-snow) using Atmospheric Environment Service records from the nearest station. Separation of peak flows according to generating process has assisted interpretation of peak flow generation in both southern (Irvine and Drake 1987) and northern Ontario (Woo and Waylen 1984) and examination of peak flow responses to forest cover changes in southern Ontario (Buttle 1994). An 8-day antecedent rainfall index (ARI) was calculated for the peak flow for each basin by summing all rain falling on the basin on the date of the peak flow and for the 7 days preceding this date. An 8-day period was also used in Woo and Waylen's (1984) analysis of floods in northern Ontario to account for the significant time lag between water inputs (snowmelt or rainfall) and flood occurrence at the Water Survey of Canada stations resulting from the large basin size and ample wetland storage. Peaks were separated according to generating event assuming that events between Julian days 1 and 140 and with 8-day ARI < 25 mm were snowmelt events, events between Julian days 1 and 140 and with 8-day ARI > 25 mm were rain-on-snow events, and all other events were rainfall events.

Flow duration curves (FDCs, cumulative frequency curves showing the fraction of time that specified daily runoffs were equaled or exceeded for a period of record) were determined annually for each of the unregulated basins for 1986–1993.

Results

Forest disturbance

The 1990 TM image classified 1501 km^2 of the area in the west-central portion of the Moose River basin (Fig. 1) as recent cutovers. However, 559 km^2 of these recent cutovers were classified as cutovers in the 1985 MSS image. Removal of these areas from the 1990 recent cutovers gave an estimated harvested area of 942 km^2 between 1985 and 1990. This was within ~10% of the observed harvested area of 1047 km^2 during the same period. Thus, our approach ap-

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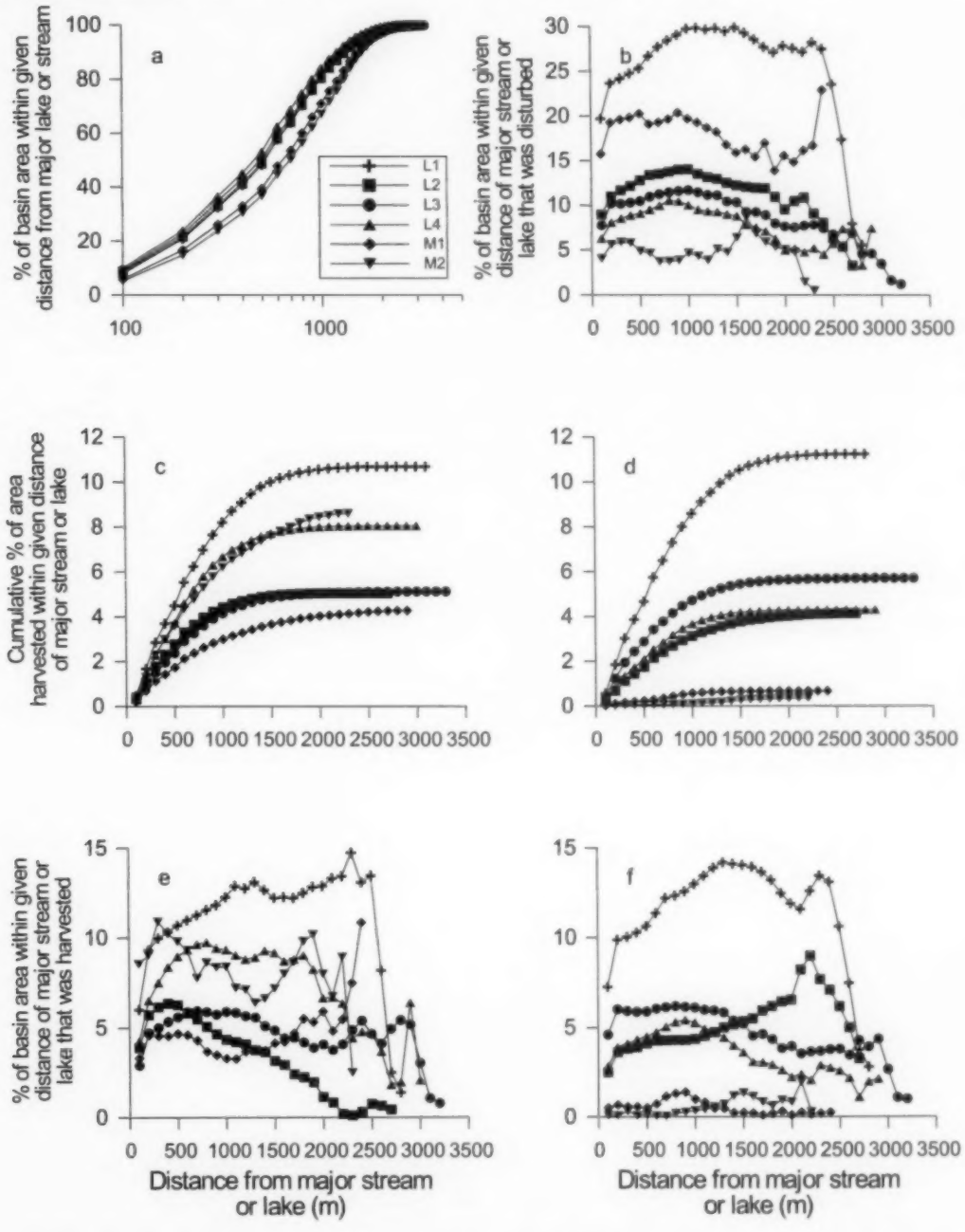
Fig. 3. (*a*) Percentage of basin area within a given distance of a major stream or lake, (*b*) percentage of basin area within a given distance of a major stream or lake that had been disturbed as of 1990, (*c*) cumulative percentage of basin area that had been harvested as of 1985 within a given distance of a major stream or lake, (*d*) cumulative percentage of basin area that had been harvested between 1985 and 1990 within a given distance of a major stream or lake, (*e*) percentage of basin area within a given distance of a major stream or lake that had been harvested as of 1985, and (*f*) percentage of basin area within a given distance of a major stream or lake that had been harvested between 1985 and 1990.


a
% of basin area within given distance from major lake or stream
L1
L2
L3
L4
M1
M2
b
% of basin area within given distance of major stream or lake that was disturbed
c
Cumulative % of area harvested within given distance of major stream or lake
d
e
% of basin area within given distance of major stream or lake that was harvested
f
Distance from major stream or lake (m)
Distance from major stream or lake (m)

pears to provide reasonable estimates of forest disturbance between 1985 and 1990 in the basins.

There were large differences in the amount and nature of forest disturbance between basins for a given year and between years for a given basin (Fig. 2; Table 3). Prior to 1985, L1, M2, and L4 showed the greatest degree of forest

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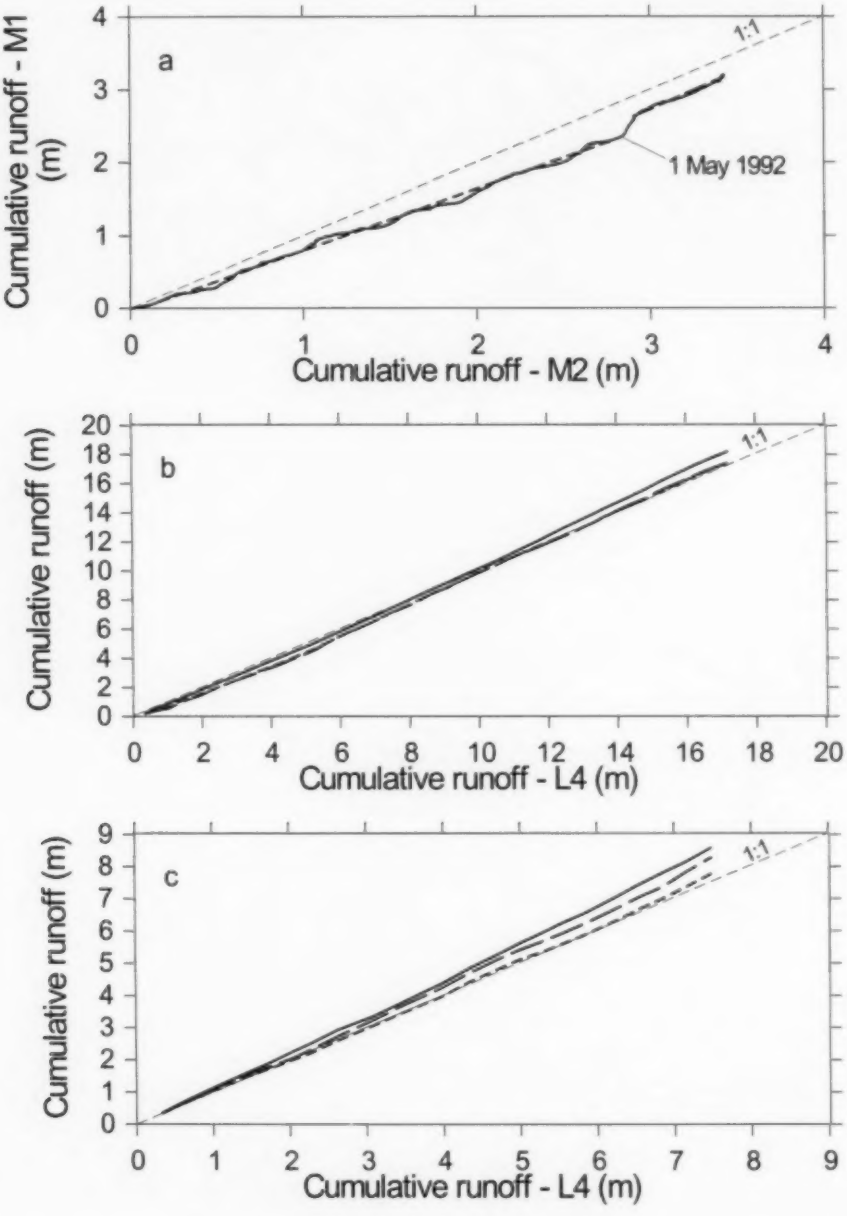
Fig. 4. DMCs of cumulative runoff: (*a*) M1 versus M2 (1986–1993) and linear best fits to the DMC for the 1 January 1986 – 1 May 1992 (thick short-dashed line, $Y = 0.845X - 0.048$, $r^2 = 0.997$) and 1 June 1992 – 14 September 1993 (thick long-dashed line, $Y = 1.038X - 0.385$, $r^2 = 0.983$) periods and L1 (thick long-dashed line), L2 (thick short-dashed line), and L3 (solid line) versus L4 for the (*b*) 1920–1966 and (*c*) 1970–1993 periods.



disturbance. However, only 0.2% of M2 was harvested between 1985 and 1990, while 6.7% of L1 was harvested during the same period. Total disturbance (harvesting between 1985 and 1990 plus old burns and cutovers on the 1990 TM image plus cutovers from the 1985 MSS image classed as recent cutovers on the 1990 TM image) generally declined from west to east across the study area: M1 (18.9%), L1 (25.2%), L2 (12.4%), L3 (10.8%), L4 (8.6%), and M2 (4.9%).

Harvesting intensity on major physiographic units varied between basins. For large basins, the proportion of harvesting between 1985 and 1990 on upland areas was 20 (L1), 67 (L2), 57 (L3), and 70% (L4). Most harvesting in L1 (61%) occurred on lacustrine plain. Of the medium basins, 90% of

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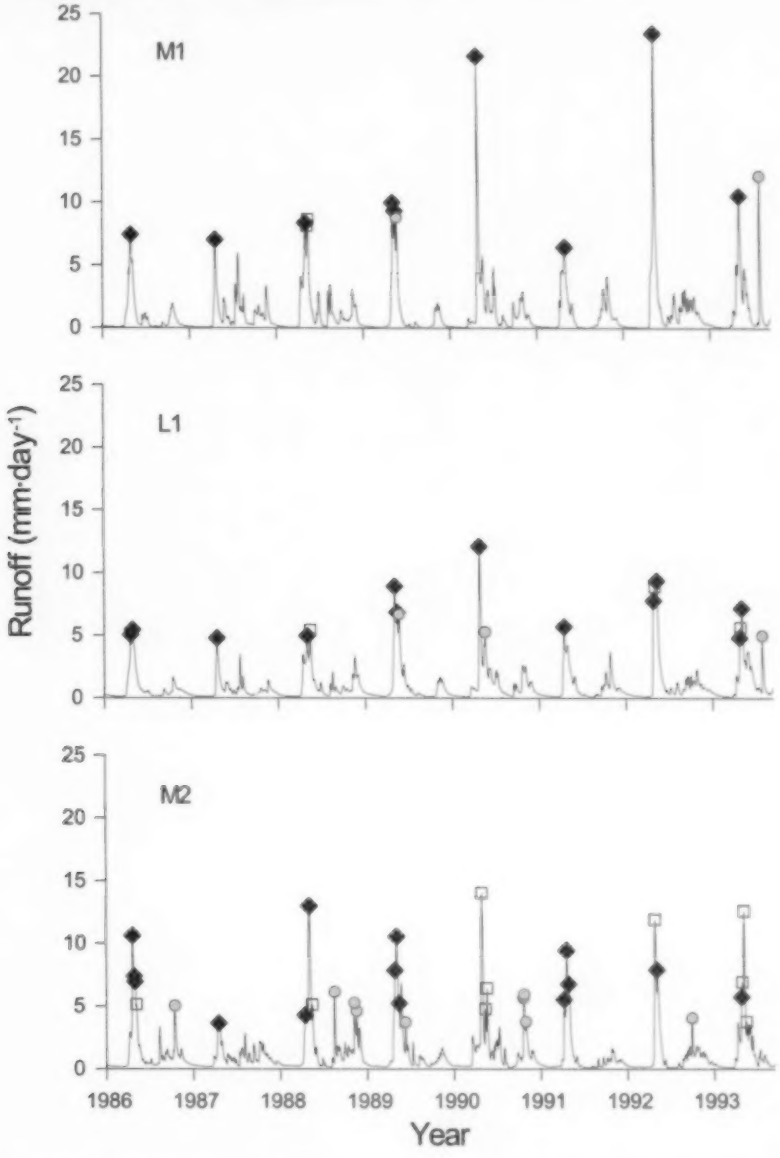
Fig. 5. Daily mean runoffs for M1, L1, and M2 (1986–1993) and type of event (diamonds, snowmelt; squares, rain-on-snow; circles, rainfall) that generated each peak flow in the partial duration series.



harvesting between 1985 and 1990 occurred on till plain and 10% on lacustrine plain in M1. This pattern was reversed in M2, where 98% of harvesting was on lacustrine plain and only 2% on till plain.

The proportion of basin area within 1 km of major streams or lakes was greater for large compared with medium basins (Fig. 3*a*), suggesting that harvesting in large basins will also tend to be relatively closer to major water bodies. This was supported by the 1985 Landsat image, where the fraction of total harvesting within 1 km of major water bodies (Fig. 3*c*) ranged from 0.77 to 0.85 for large basins but was only 0.7 and 0.72 in M1 and M2, respectively. The fraction of total harvesting between 1985 and 1990 within 1 km of major streams and lakes was similar to 1985 results for large basins (Fig. 3*d*); however, it increased to 0.84 for M1 while declining to 0.29 for M2.

Distribution of harvesting intensity within each basin was determined by dividing the amount of harvesting within a given distance interval from major water bodies by the basin area within that distance interval (Figs. 3*e* and 3*f*). In almost all cases, harvesting intensity of basin area within 100–200 m of major streams and lakes was greater than that within 0–100 m. This may reflect the presence of buffer strips, which can extend 30–90 m from streams or lakes (R. Mackereth, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ont., personal communication) and in which

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Table 4. Slope coefficients for linear regression equations fit to DMCs relating cumulative WY runoff from L1, L2, and L3 to cumulative runoff from L4.

Time period	L1 vs. L4	L2 vs. L4	L3 vs. L4
1920–1966	1.051[a] (0.00%)	1.042[a] (0.00%)	1.074[a] (0.00%)
1970–1993	1.094[a,b] (4.09%)	1.027[a,c] (–1.44%)	1.143[a,b] (6.42%)
1970–1984	1.086[a,b] (3.33%)	1.014 (–2.69%)	1.115[a,b] (3.82%)
1985–1993	1.177[a,b,d] (11.99%)	1.103[a,b,d] (5.85%)	1.201[a,b,d] (10.57%)

Note: Coefficients of explanation (r^2) for all equations were >0.99. Values in parentheses indicate percent change in slope coefficient relative to the coefficient for the 1920–1966 period, i.e., ((coefficient for period x – coefficient for 1920–1966)/coefficient for 1920–1966) × 100%.

[a]Significantly greater than 1 ($p < 0.05$).
[b]Significantly greater than slope coefficient for the 1920–1966 period ($p < 0.05$).
[c]Significantly less than slope coefficient for the 1920–1966 period ($p < 0.05$).
[d]Significantly greater than slope coefficient for the 1970–1984 period ($p < 0.05$).

Table 5. Daily mean runoffs (mm·day^{-1}) corresponding to various flow durations, 1986–1992.

		% of time daily mean runoff equaled or exceeded						
Basin	Year	1	5	10	25	50	75	100
M2	1986	9	5	2.9	1.15	0.58	0.305	0.17
	1987	3.4	2.4	1.95	1.1	0.7	0.31	0.17
	1988	11	5.05	4	1.7	0.7	0.28	0.11
	1989	9.2	6	3.9	1.05	0.5	0.28	0.19
	1990	11.5	5.1	3.3	1.9	0.9	0.28	0.108
	1991	8.3	5.1	1.7	0.74	0.33	0.2	0.076
	1992	10.5	5.9	2	1.05	0.41	0.18	0.084
M1	1986	6.6	4.1	1.8	0.79	0.19	0.072	0.03
	1987	6.3	3.4	2.4	1.35	0.53	0.08	0.031
	1988	8.1	5.7	3.2	1.5	0.59	0.14	0.03
	1989	9	7	2.05	0.53	0.14	0.065	0.013
	1990	16	4.6	3.05	1.55	0.57	0.16	0.039
	1991	6.05	4.3	3	1.4	0.24	0.065	0.004
	1992	19	5.9	3	1.7	0.69	0.105	0.037
L1	1986	5.4	3.7	2	0.695	0.37	0.17	0.083
	1987	3.5	2	1.15	0.73	0.47	0.2	0.105
	1988	5	3.35	2.75	1.3	0.59	0.205	0.105
	1989	8.05	6	2.6	0.975	0.325	0.2	0.105
	1990	10	4.05	2.5	1.6	0.69	0.24	0.11
	1991	5.4	3.6	2.3	1.05	0.37	0.2	0.073
	1992	8.9	7.5	2.1	1.2	0.67	0.3	0.115

harvesting is generally not permitted. Some basins showed consistent patterns between the two images; for example, harvesting intensity in L1 increased with distance from water bodies up to ~2.5 km and dropped markedly beyond that distance. In other cases, the degree of harvesting intensity with distance from major water bodies changed with time. Thus, the greatest harvesting intensity in L2 as of 1985 was on areas ~500 m from streams and lakes, with disturbance decreasing with distance. The 1990 image showed the reverse pattern, with harvesting intensity increasing with distance from streams or lakes and peaking at ~2.2 km. Despite this shift, distribution of total disturbance as of 1990 (Fig. 3*b*) in L2 was relatively uniform with distance from major water bodies. Harvesting between 1985 and 1990 in M1 and M2 was minor (Fig. 3*d*). However, intensity of total disturbance was much greater in M1 (Fig. 3*b*), where >15% of the basin within 1 km of major water bodies was disturbed by 1990, most of this in the form of old burns and cutovers.

The nature of harvesting within basins changed with time (Table 3). Mean patch size of harvested areas decreased from 1985 to 1990 in all basins, while number of patches and patch density increased in all but M2. The latter is consistent with the decrease in harvesting in this basin during the ~5-year period. Patches comprising 1990 old burns and cutovers plus 1985 cutovers classed as 1990 recent cutovers generally showed the least patch contiguity in any given basin. The exception was M2, where the 1985 cutover patches were the least contiguous of any disturbed areas in the basin. The 1990 image indicated that patches harvested between 1985 and 1990 in L1 were the least contiguous of any of the basins, with 1985 cutover patch contiguity being greatest in M1 and M2. However, the range in CVN values for 1985–1990 harvested patches between basins was small (0.025–0.510) relative to the potential range (0–8).

Streamflow response

Runoff

There was good agreement between cumulative daily run-

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off from the M1 and M2 basins from 1 January 1986 to 1 May 1992 (Fig. 4*a*), with cumulative runoff from M1 averaging ~85% of that from M2. This relationship changed following a large event beginning 1 May 1992 in M1 (Fig. 5), when M2 generated comparatively less runoff during this 31-day period. The slope of the DMC increased significantly following 1 June 1992, such that cumulative runoff from M1 was ~4% higher than that from M2. Conversely, the DMC of cumulative precipitation for M1 versus M2 (not shown) remained linear during the 1986–1992 period.

Shifts in DMC relationships for large basins between periods (Figs. 4*b* and 4*c*; Table 4) may have resulted from systematic temporal trends in runoff from L4 due to climatic variations and (or) land-use changes. However, time series analysis of WY runoff from L4 showed no significant temporal trend during either the 1920–1966 or 1970–1993 period, which supported use of L4 as a "quasi-control" basin. DMCs of cumulative WY precipitation (not shown) indicated that precipitation in L4 generally equaled or exceeded that in L1, L2, and L3 for both the 1920–1966 and 1970–1993 periods. Cumulative runoff from L3 exceeded that from other basins during each period. The reason for this is unknown, although it is consistent with L3's higher mean runoff/precipitation ratio relative to the other basins (Table 2).

Slope coefficients of linear best fits to DMCs from all basins were significantly >1 for all periods, with the exception of the slope coefficient for L2 versus L4 for the 1970–1984 period. Thus runoff from L1, L2, and L3 generally exceeded that from L4. This difference was most pronounced for the 1985–1993 period, and DMC slopes ranged from 5.85 (L2) to 11.99% (L1) greater than the slope of the corresponding curve for the 1920–1966 period. The increase in WY runoff relative to that expected from the 1920–1966 period can be predicted using the 1985–1993 DMC slopes, assuming a mean WY runoff of 351 mm for L4 (Table 2). Thus, WY runoff would be 44 (L1), 21 (L2), and 45 mm (L3) greater than that estimated by the DMC slopes for the 1920–1966 period.

WY runoff ratios

There were no significant temporal trends in the ratio of WY runoff to WY precipitation for medium or large basins, either for original ratios or for differences in ratios between basins. Total precipitation, total snowfall, or the fraction of WY precipitation consisting of snowfall did not explain a significant amount of the variation in runoff ratios for each basin.

Peak flows

Annual maxima in M2 were generated by snowmelt in 1986, 1987, 1988, 1989, and 1991 and by rain-on-snow in the remaining years (Fig. 5). Annual maxima at the start of the period were similar to those at the end, with no apparent temporal trend. Rainfall generated a larger number of peak flows for M2 than for M1 and L1. Most annual maxima in M1 were generated by snowmelt. The major exception was the rainfall-generated annual maximum in 1993, while rain-on-snow peak flows occurred only in 1988. Snowmelt in 1990 and 1992 generated annual maxima approximately twice those observed at the beginning of the period; however, there was no statistically significant temporal trend in the snowmelt peak flows. L1 showed a similar pattern to that of M1. Annual maxima were generated by snowmelt in almost all years, while rain-on-snow resulted in only one annual maximum flow (1988). Snowmelt in L1 also tended to generate larger peak flows later in the period relative to those seen in 1986, 1987, and 1988; however, no statistically significant trend was observed with time.

FDCs and timing of annual minimum flows

Daily mean runoffs corresponding to various flow exceedance levels were abstracted from the annual FDCs for M1, L1, and M2 (Table 5). Runoff at a given exceedance level for a particular year was expressed relative to runoff at the same exceedance level in 1986:

$$(1) \qquad \text{Ratio}_{\text{year } x} = \frac{\text{Runoff}_{\text{year } x} - \text{runoff}_{1986}}{\text{Runoff}_{1986}}$$

Ratios were determined for the 100, 75, 50, 25, 10, 5, and 1% exceedance levels. The mean ratio for M2 for all years was not significantly different from 0 for any flow exceedance level, and there were no statistically significant temporal trends in any ratios. Temporal trends in ratios for both M1 and L1 were also statistically insignificant. Mean ratios at the largest and smallest flow exceedance levels (1, 5, 75, and 100%) in M1 were not significantly different from 0 (difference of means t test); however, mean ratios were significantly >0 at the 10, 25, and 50% levels. This indicates that there had been in increase in moderate flows in the basin during the 1986–1992 period. Mean ratios at the 1, 5, 10, and 50% exceedance levels in L1 were not significantly different from 0. However, mean ratios were significantly >0 at the 25, 75, and 100% levels, indicating an increase in moderate and low flows during the 1986–1992 period.

Annual minima between 1986 and 1993 occurred either in mid- to late summer or in late winter, immediately before the onset of spring snowmelt. There was good agreement (within 1 or 2 days) between the dates of occurrence of annual minimum flow for M1 and L1. This is not surprising given the proximity of the basins. The date of annual minimum flow for these two basins and M2 agreed to within a few days in four out of eight years. There was no systematic difference between the two western basins and M2 in the remaining years. Annual minima occurred in late winter in M1 and L1 and in mid- to late summer in M2 in some years, while the reverse occurred in other years. There was also no significant correlation between annual variations in magnitude of minimum flows from the basins between 1986 and 1993.

Discussion

Most of the recent forest disturbance in the boreal forest of northeastern Ontario has resulted from harvesting, while fire (either natural or as prescribed burns) was of minimal significance at the spatial scale examined here. Harvesting patterns have changed in recent years, with mean cutblock size decreasing from 1985 to 1990. Southeastern basins in the study area experienced either no change or a decrease in harvesting activity (as a percentage of basin area) during the 1985–1990 period. Conversely, harvesting increased in other basins during this period, particularly in the northwest part

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of the study area. The small range in CVN values for 1985–1990 harvested patches between basins suggests that recent harvesting in the study area involved small but relatively contiguous cutblocks that have produced a low degree of landscape fragmentation. Sachs et al. (1998) reported a similar situation in interior British Columbia, where the landscape is in the early stages of fragmentation as a result of harvesting.

Assessment of the impacts of forest disturbance on streamflow in this region is complicated by the large basin sizes, flow regulation and limited streamflow records for some basins, lack of proper control basins, limited extent of forest disturbance, and availability of data on forest disturbance for only two instants in time. Thus, we did not observed significant changes in such properties as runoff/precipitation ratios that have been noted for small basins elsewhere in the boreal forest (e.g., Bayley et al. 1992).

Nevertheless, recent forest disturbance appears to be associated with some aspects of streamflow from medium and large basins in the region. Increased runoff from M1 relative to M2 following 1 May 1992 reflects the greater proportion of M1 that was disturbed as of 1990 (18.9 versus 4.9%). The shift in the runoff DMC for M1 versus M2 was likely not the result of changes in relative precipitation inputs to the basins, which were fairly constant during the1986–1992 period. However, this change cannot be attributed to forest disturbance with great confidence, due to brevity of the hydrological record and lack of data on temporal changes in forest disturbance in M1 during the 1985–1990 period.

Equivocal links between forest disturbance and runoff were also apparent for the large basins. L1, L2, and L3 all demonstrated increased runoff relative to L4, particularly during the 1985–1995 period. However, these basins did not experience increased precipitation inputs relative to those for L4. Total disturbed area as of 1990 in L4 was 8.6% of basin area. Disturbance in the other large basins in excess of this "quasi-control" value was 2.2 (L3), 3.8 (L2), and 16.6% (L1). These forest cover changes are below the 20–25% threshold that must be met or exceeded to detect a measurable response in annual runoff to forest disturbance (Bosch and Hewlett 1982; Hornbeck et al. 1993). Nevertheless, Trimble et al. (1987) and Buttle (1994) documented significant changes in annual runoff for changes in forest cover below this threshold. The increase in DMC slope for L1 is consistent with total forest disturbance, concentration of harvesting in the basin on the lacustrine plain with its comparatively low infiltration rates, mean cutblock patch size, and recent harvesting intensity in near-stream areas in L1 relative to the other large basins. The 44-mm increase in WY runoff is also bracketed by a 23-mm increase predicted for a 10% reduction in coniferous forest cover (Sahin and Hall 1996) and by a 100-mm increase in annual runoff following clear-cutting of small (<4.5 km^2) boreal forest basins in north-central Ontario (Nicolson 1995). However, the slight differences in 1985–1990 harvesting activity and total disturbance between L2, L3, and L4 appear insufficient to account for the increased cumulative runoff for L2 and L3 relative to L4 during the 1985–1993 period. Increased runoff from L2 and L3 was also unrelated to distribution of recent harvesting or total disturbance with respect to major water bodies, which was similar for L2, L3, and L4. Despite the results of time series analysis of WY runoff from L4, climate change may have influenced the runoff response of the large basins. Thus, the increased WY runoff from L1 cannot be attributed to forest disturbance in the basin. Paterson et al. (1998) suggested that hydrological changes induced by climatic variations in the boreal forest may override those due to forest disturbance such as harvesting or fire for small basins, and this should be examined in future work at larger spatial scales.

Forest disturbance did not produce significant changes in peak flows in this region, regardless of the nature of the generating event. Cheng (1989) found increases in spring runoff following clear-cutting in interior British Columbia to be related to the amount of rainfall and snowmelt during April and May (Cheng 1989). We do not have information on snowmelt rates in each basin during the 1986–1993 period, and no relationship was found between the size of snowmelt-generated peak flows and snowfall during the preceding winter. Nevertheless, the similarity in annual maxima generated by snowmelt and rain-on-snow between 1986 and 1993 for M2 suggests no significant interannual changes in the intensity of snowpack ablation during this period. It may be reasonable to assume that the meteorological conditions that drive snowmelt and that are relatively independent of forest cover conditions (i.e., incoming solar radiation, rainfall, air mass wind speed, temperature, and relative humidity) are relatively similar between the basins in a given year. Thus, there is some association between the degree of forest disturbance and increases in the size of snowmelt peak flows for some years in M1 and L1. However, the change in peak flows is not as conclusive as demonstrated elsewhere (e.g., Verry et al. 1983; Cheng 1989), which may reflect the large size of the study basins combined with the relatively small fraction of the basins that were disturbed between 1985 and 1990. Rapid snowmelt runoff from disturbed areas may simply have been subsumed by the hydrological response of the large undisturbed portion of the basins.

All three basins had multiple flood peaks during snowmelt in most years, which might reflect the disturbance that all basins had undergone prior to 1986. M2 had multiple flood peaks in all but one snowmelt period, thus providing the clearest demonstration of desynchronization of flood peaks (cf. Verry et al. 1983). In addition to disturbance by harvesting, roughly 9% of M2 was impacted by urban development, agriculture, and mining as of 1990 (Buttle et al. 1998). Snowmelt in these open areas, superimposed on the clay-rich soils that dominate the basin, appeared to produce a streamflow peak that preceded that due to melt in forested parts of M2. Despite forest disturbance in M1 and L1 between 1985 and 1990, we found no evidence for increasing desynchronization of flood peaks during snowmelt. There was also no advance in the date of the initial snowmelt peak flow from any of the basins between 1986 and 1993. As with peak flow magnitude, the basins may have been too large to detect the effect of disturbance on peak flow timing.

The FDC analyses suggest that the minor forest disturbance in M2 between 1985 and 1990 did not result in significant changes in streamflow. As with the partial duration series, the FDCs indicate that while peak flows for M1 and L1 had increased in some years during the mid- to latter part of the 1986–1993 period, there were no significant temporal

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trends. Timing of low flows was also independent of the degree of basin disturbance. Nevertheless, forest disturbance in M1 and L1 was associated with increases in small and moderate flows. This is consistent with studies (e.g., Hornbeck et al. 1993; Keenan and Kimmins 1993; Hartman et al. 1996) showing clear-cutting to produce the greatest streamflow increases during low-flow periods, with smaller impacts on peak flows. The results also support the scale effect in the relationship between forest disturbance and resulting streamflow changes suggested by Coats and Miller (1981). Thus, disturbance was associated with increased moderate flows in the medium basin but mainly with low flow increases in the large basin. These increases generally occurred during the summer, and the associated changes in flow levels may have important implications for aquatic communities in these rivers. This scale dependence of the hydrological response to disturbance requires further study and should be considered when assessing the cumulative impact of forest disturbance on the hydroecology of large river systems.

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Impacts of intensive harvesting on hydrology and nutrient dynamics of northern hardwood forests

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Abstract: Whole-tree clear-cutting and progressive strip-cutting of northern hardwood forests at the Hubbard Brook Experimental Forest in central New Hampshire resulted in measurable changes in physical and chemical conditions of forest streams. As a result of reduced transpiration and interception, water yield for the first year after whole-tree harvesting increased by >150 mm, the majority of which occurred during the growing season. Peak flows increased only moderately. Water yield and peak flow increases disappeared within 4–6 years as a result of rapidly regrowing vegetation. Sediment yields increased during and after harvesting but can be maintained within normal ranges of reference streams by careful use of best management practices. Stream chemistry changes occurred immediately following harvesting, most notably in the form of increases in concentrations of Ca^{2+}, K^+, NO_3^-, and H^+. The concentrations return close to preharvest levels within 3–5 years. The above changes are discussed in terms of their causes and implications for aquatic habitat and fisheries.

Résumé : La coupe à blanc des arbres entiers et l'exploitation progressive par bandes de forêts de feuillus nordiques à la forêt expérimentale de Hubbard Brook, dans le centre du New Hampshire, se sont traduites par des changements mesurables dans les conditions physiques et chimiques des cours d'eau forestiers. Suite à la réduction de la transpiration et de l'interception, les apports d'eau pour la première année après l'exploitation des arbres entiers a augmenté de >150 mm, la plus grande part de cette augmentation se produisant pendant la saison de croissance. Les débits maximaux n'ont augmenté que modérément. Les augmentations des apports d'eau et des débits maximaux ont disparu au bout de 4 à 6 ans du fait de la régénération rapide de la végétation. Les apports de sédiments ont augmenté pendant et après l'exploitation, mais peuvent se maintenir dans les plages normales des cours d'eau témoins grâce à l'utilisation prudente des meilleures pratiques de gestion. Des changements dans la chimie des cours d'eau se sont produits immédiatement après la coupe, et principalement sous forme d'augmentation des concentrations de Ca^{2+}, K^+, NO_3^- et H^+. Les concentrations reviennent à un niveau proche de celui de la période préexploitation au bout de 3–5 ans. Nous analysons les changements ci-dessus dans l'optique de leurs causes et de leurs incidences pour l'habitat aquatique et les pêches.

[Traduit par la Rédaction]

Introduction

Northern hardwood forests provide a variety of amenities and services including high quality water, wildlife habitat, timber products, recreational opportunities including fisheries, and watershed protection (Hornbeck and Leak 1992). Forestry operations, particularly harvesting, can have negative impacts on these amenities, especially water. The 1972 Federal Water Pollution Control Act Amendments classified silvicultural practices as potential nonpoint sources of water pollution to be controlled by best management practices (BMPs) (Dissmeyer 1994). As a result, forest owners, forest managers, and loggers need to be concerned about the effects of harvesting operations on stream water quantity and quality and aquatic biota (Guimier 1998).

In this paper, we present long-term results from two watersheds in the northern hardwood forest of the Hubbard Brook Experimental Forest (HBEF). One watershed was clear-cut from 1970 to 1974 using a shelterwood practice known as progressive strip-cutting. The other was mechanically whole-tree clear-cut in 1983–1984. When the preharvest calibration is included, these watershed experiments have been in progress since the early 1960s. Various results have been published during the study period. Effects on water quantity, including annual and seasonal yields, low flows, and storm peaks, were published by Hornbeck et al. (1997). Impacts on hydrologic and nutrient cycles during the first 10 years after strip-cutting were published by Hornbeck et al. (1986), and Martin and Hornbeck (1994) have reported effects on soil disturbance and sediment yield for the early years after whole-tree clear-cutting. This paper adds more years of data to these earlier reports and carries the results and comparisons between the two watersheds further into the period of forest recovery and development. We also make use of other previously reported findings from the Hubbard Brook Ecosystem Studies to help interpret the long-term results in terms of implications for fisheries.

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Methods

HBEF is located at 43°56′N, 71°45′W in the White Mountains of central New Hampshire. It is a 3160-ha watershed established in

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Table 1. Watershed descriptions.

Watershed	Area (ha)	Elevation (m)	Aspect	Slope	Treatment
WS 3	42.4	527–732	S23°W	12.1°	Hydrologic reference
WS 4	36.1	442–747	S40°E	15.6°	Progressive stripcut
WS 5	21.9	488–762	S24°E	15.4°	Whole-tree clearcut
WS 6	13.2	549–792	S32°E	15.8°	Biogeochemical reference

1955 by the USDA Forest Service for watershed and ecosystem research. The Hubbard Brook Valley was glaciated approximately 14 000 years before present (Likens and Davis 1975). Till depths range from 0 to 5 m across the study watersheds. Soils derived from this till are fine sandy loams classified as Lithic and Typic Haplorthods. Within HBEF, nine tributary watersheds have been instrumented for hydrometeorogical monitoring. This paper will be concerned with watersheds (WS) 3, 4, 5, and 6 located on the south-facing aspect of HBEF (Table 1).

WS 3 and WS 6 are untreated reference watersheds. They are both forested with mature northern hardwoods that have not been harvested since prior to 1920 (Bormann and Likens 1979). The principal tree species include sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), and American beech (*Fagus grandifolia* Ehrh.). WS 4 was harvested as a progressive stripcut (SC), a commercial harvesting practice designed to foster yellow birch regeneration (Marquis 1966). Prior to harvesting, 49 strips, each 25 m wide, were laid out on the watershed parallel to the elevational contour and perpendicular to the stream. Strip orientation was roughly east to west. Every third strip was harvested from September 28 to October 29, 1970. From September 7 to October 1, 1972, the strips immediately adjacent and toward the south of the first set of strips were harvested. The third and final series of strips were harvested from October 1 through November 1, 1974. A variable-width (15–25 m wide) buffer of uncut trees was left on both sides of the main stream channel in an attempt to minimize solar heating, reduce nutrient loss, and prevent sediment from reaching the stream. All trees, living and dead, >2.5 cm diameter at breast height (DBH) were felled on all strips. Merchantable tree stems (at the loggers discretion) were removed from the watershed. Transportation was by rubber-tired skidders to landings outside the watershed. WS 5 was harvested as a mechanical whole-tree clearcut (WT) between October 18, 1983, and May 21, 1984. All stems >2.5 cm DBH were harvested by mechanical feller-buncher and skidded to roadside off the watershed by rubber-tired skidder. An estimated 93% of the aboveground biomass was removed from the watershed including the branches and tops. No uncut buffer strips were left along the stream channel. Logging on both watersheds adhered to the BMPs prescribed by the State of New Hampshire. The BMPs are typical of those used by all states in the northeastern United States and carefully spell out recommendations for roads, stream crossings, landings, and site stabilization after logging (Dissmeyer 1994).

The streams as they leave WS 3 and WS 4 are fitted with stream gaging stations comprising 120°, sharp-crested, v-notch weirs. The streams draining WS 5 and WS 6 are fitted with 90°, sharp-crested, v-notch weirs with modified San Dimas flumes in tandem. Precipitation is sampled with a network of standard and recording gages having a density of one gage for every 13 ha and apportioned to the watersheds using Thiessen weighting (Federer et al. 1990; Likens and Bormann 1995). A water year of June 1 through May 31 was used for summarizing and analyzing hydrologic and nutrient data. This water year was chosen because soils at HBEF are fully recharged following spring snowmelt and all snow has completely melted (Federer et al. 1990).

Soil disturbance on the WT was estimated using 81 transects measured before and after clear-cutting. The transects were 10 m long. The soil surface along each 0.1-m interval was classified into the following types: "undisturbed, depressed" where the soil surface was undisturbed but had been depressed by a wheel or falling tree, "scarified" where mineral and organic soil were mixed, "scalped" where organic horizons were scraped off the mineral soil, "mounds" of either mineral or organic soil, wheel "ruts" lined with either mineral or organic soil, "vegetation" consisting of slash or stumps, and bare "rocks" >10 cm across.

Soil disturbance on the SC was estimated, but only as disturbed or undisturbed. Disturbance was defined as any visual change in the forest floor or mineral soil caused by the logging equipment. Intensity of disturbance was not measured on the SC.

Sediment yield from the study areas was estimated by removing all of the material, organic and mineral, that had collected in the stilling basins behind the v-notches during the previous water year. This material was measured, excavated, sampled, dried, and weighed. Oven-dry weights were then calculated for all of the sediment removed from each basin and extrapolated back over the respective watershed as mass of soil material lost per unit area of the watershed. Thus, sediment measurements were on an annual basis rather than by individual storms. On the basis of intensive studies of dissolved solids and suspended sediment, Bormann et al. (1974) suggested that an additional 2% should be added to these values to account for particulates that flowed over the notches during high flows and that 25% should be added to account for suspended sediment. The data presented here do not include these additions. More details of the methods used to determine the degree of soil disturbance, erosion, and sediment yield may be found in Martin and Hornbeck (1994).

Statistical analyses

Effects of treatments on water yield and nutrient budgets were tested using the paired watershed approach. Linear regression equations were developed for water quantity parameters, annual sediment yield, and nutrient outputs between the reference watersheds and each treated watershed for the years of record before treatment. After treatment, water, sediment, and nutrient outputs from the reference watersheds were inserted into the equations to estimate values for the treated watershed as if it had not been treated. Differences between measured parameters following treatment and these untreated estimates were considered to be statistically significant if they exceeded the 95% confidence intervals around the paired pretreatment calibration data. Reinhart (1967) and Hewlett et al. (1969) present more details on the paired watershed approach and its applicability for studies such as we report. No significance testing could be done on the sediment yield data from the SC because of lack of precutting calibration data. The impacts of harvesting on concentrations of nutrients in stream water were determined by viewing long-term plots of weighted, monthly means. Postharvest differences between the reference and treated watersheds were usually quite obvious in terms of occurrence, magnitude, and duration, and statistical testing was deemed unnecessary.

Nutrient determinations and calculations

Bulk precipitation has been collected and analyzed for the major inorganic ions since 1963 (Likens and Bormann 1995). Stream water has been collected weekly by grab samples just above the stream gaging stations since 1963 and, also, analyzed for the major

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Table 2. Changes in annual water yield for harvested watersheds.

	Stripcut			Whole-tree harvest		
		Change due to treatment			Change due to treatment	
Year after initial treatment	Estimate if untreated (mm)	mm	%	Estimate if untreated (mm)	mm	%
1	777	22	3	648	152*	23
2	1032	46*	4	876	47	5
3	1417	114*	8	806	–15	–2
4	819	67*	8	742	–11	–1
5	1263	55*	4	681	4	1
6	868	82*	9	1020	46	5
7	1042	69*	7	1086	51*	5
8	870	–14	–2	835	66*	8
9	725	–30*	–4	860	47	5
10	769	–26*	–3	879	20	2
11	1144	–18	–2	605	21	3
12	869	–45*	–5	818	46	6
13	1069	–33	–3	1150	64*	6
14	709	–21*	–3	747	–5	–1
15	927	–44*	–5			
16	856	–67*	–8			
17	779	–29	–4			
18	702	–59*	–8			
19	1079	–42*	–4			
20	1158	–63*	–5			
21	904	–42*	–5			
22	943	–60*	–6			
23	918	–30*	–3			
24	623	–36*	–6			
25	1362	–23	–2			
26	1180	–18	–2			
27	768	–66*	–9			

Note: *significant difference ($p < 0.05$).

inorganic ions (Likens and Bormann 1995). Concentrations of Ca^{2+}, Mg^{2+}, Na^{+}, and K^{+} were measured by flame atomic absorption spectrophotometry with a detection limit of 0.01 mg·L^{-1} and a sensitivity of 0.01 mg·L^{-1}, H^{+} was measured as pH potentiometrically with glass electrodes in the laboratory, SO_4^{2-} was measured by automated, colorimetric, barium sulfate, methylthymol blue technique with a detection limit of 0.1 mg·L^{-1} and a sensitivity of 0.2 mg·L^{-1} before 1976 and by ion chromatography with a detection limit of 0.05 mg·L^{-1} and a sensitivity of 0.2 mg·L^{-1} beginning in 1976, and NO_3^{-} was measured by automated, colorimetric copper–cadmium reduction, diazo-complex technique with a detection limit of 0.01 mg·L^{-1} and a sensitivity of 0.05 mg·L^{-1} prior to 1976 and by ion chromatography with a detection limit of 0.005 mg·L^{-1} and a sensitivity of 0.01 mg·L^{-1} beginning in 1976. Stream water from the study watersheds is colorless except for infrequent episodes of sediment, and dissolved organic C values are generally <2.0 mg·L^{-1} from both reference and harvested watersheds. Nutrient budgets were developed by combining ionic concentrations with volumes of precipitation and stream water to calculate the mass of a nutrient per unit area (Likens and Bormann 1995).

Results

Water yield and flow levels

Water yield increases for the SC, which was cut in thirds over a 4-year period, were rather modest. For years 2–4 during and years 5–7 following the SC, there were significant increases in annual water yield ranging from 4 to 9% (Table 2). As regeneration proceeded, water yield actually decreased 3–9% below levels from the uncut reference watershed. These decreases have persisted from year 9 after cutting to date.

Water yield increased 23% the first year following the WT. There were also significant increases of 5–8% during years 7, 8, and 13 following cutting. Otherwise, there were no significant changes in water yield resulting from this intensive harvest. Fourteen years of regeneration have not produced any significant decreases in water yields from the WT (Table 2).

The water yield increases occurred primarily as augmentation to low flows during the growing season. Complete recharge of soil moisture usually occurs in mid- to late autumn at HBEF, and transpiration-induced decreases in stream flow seldom extend into the dormant season. Depending on antecedent soil moisture, peak flows during the growing season can be increased by up to 60% in the first 1–2 years after harvest. Any increases in peak flow rates quickly disappear with the restablishment of a new forest (Hornbeck et al. 1997). Total snowmelt runoff was largely unaffected by the harvests, but timing was changed. In the absence of shade provided by branches and stems, snowmelt and snowmelt

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Table 3. Soil disturbance due to whole-tree clear-cutting.

Type of disturbance	%	SE
Undisturbed	30	3
Depressed (undisturbed but compressed by equipment)	4	1
Scarified (organic and mineral soils mixed)	13	1
Scalped (organic pad scraped from mineral soil)	1	1
Organic mounds (mounds of organic soil)	13	2
Mineral mounds (mounds of mineral soil)	6	1
Organic ruts (wheel ruts lined with organic soil)	10	1
Mineral ruts (wheel ruts into mineral soil)	18	3
Vegetation (stumps and logging slash)	2	1
Bare rocks (rocks >10 cm in diameter)	3	1
Total	100	

runoff were advanced by up to 17 days compared with the uncut reference watershed (Hornbeck et al. 1997).

The amount and duration of water yield changes at HBEF are determined in large part by differences in how the forests were cut and how rapidly the new forests regenerate. Harvesting of the SC was spread over 4 years, allowing regeneration to develop on adjacent strips during harvesting and for some of the water yield increases from cut strips to be utilized by the uncut strips and by the buffer strips. As a result, annual water yield increases from the SC were small and short-lived (Table 2). The WT was harvested in one large block, hence the larger initial increase in annual water yield. However, the regrowing forest reduced the water yield increases by more than half in the second year after harvest (Table 2).

From year 8 after harvest to the present, the SC has yielded less water than the uncut reference watershed (Table 2). This change is due to the regeneration having substantial numbers of pioneer plant species that have lower stomatal resistances and greater transpiration than species in mature northern hardwood forests (Hornbeck et al. 1997). As the pioneer species drop from the stand in the future, transpiration is expected to decrease and stream flow should eventually return to preharvest levels. An extended period of decreases in water yield has not occurred after WT (Table 2). Possible explanations are greater area of watershed in skid trails that were slow to regenerate, reductions in regeneration due to browse by moose (moose populations have only recently irrupted at HBEF), and prolific sprouting of beech and sugar maple, which have greater stomatal resistances than pioneer species (Hornbeck et al. 1997).

Sediment yield

The WT at HBEF caused considerable soil disturbance (Table 3). Thirty percent of the watershed area remained undisturbed, with 70% disturbed by the harvest to some degree. Disturbance ranged from nearly 4% of the entire watershed having the forest floor intact but depressed by one pass of logging equipment to 18% covered with wheel or track ruts into mineral soil. Logging disturbed the forest floor organic horizons to the point where nearly 28% of the WT exhibited bare mineral soil (including classes scalped, mineral mounds, mineral ruts, and bare rocks) (Martin and Hornbeck 1994). Thirty-three percent of the soil of the SC was undisturbed, with 67% disturbed to some degree.

Soil disturbance during logging can lead to erosion and deposition of sediment into streams. However, erosion and sediment yield are natural geologic processes that are markedly ameliorated by biotic factors in forest ecosystems (Bormann et al. 1969). Annual sediment yield from uncut reference watersheds varied widely from 3 to 71 kg·ha^{-1} (WS 3) and from 1 to 95 kg·ha^{-1} (WS 6) (Table 4). Sediment yield from the SC ranged from 3 to 146 kg·ha^{-1}. The highest value occurred during the water year when the second series of strips were cut. Sediment yield from the stream in the WT ranged from 3 to 208 kg·ha^{-1}. Sediment yields from this watershed prior to harvest had been as great as 134 kg·ha^{-1}. Significant increases did occur the first 3 years after cutting and in year 12 (Table 4).

Table 4. Sediment yield (kg·ha^{-1}) from four watersheds at HBEF.

Water year	WS 3	WS 6	WS 4	WS 5	WS 6 precipitation (mm)
1970[b]	—	42	3[a]	—	1360
1971	—	5	13[a]	—	1329
1972[c]	—	6	27[a]	—	1280
1973	—	95	146[a]	—	1565
1974[d]	—	25	16[a]	—	1888
1975	35	18	67	24	1308
1976	10	15	6	12	1769
1977	29	79	132	134	1402
1978	37	18	65	68	1532
1979	47	25	30	97	1362
1980	64	32	38	89	1194
1981	25	34	36	41	1355
1982	28	10	27	35	1585
1983[e]	11	3	5	14	1410
1984[e]	47	35	52	64	1638
1985	5	4	10	112*	1200
1986	45	17	77	129*	1425
1987	71	52	89	208*	1311
1988	4	1	10	6	1290
1989	19	7	35	15	1234
1990	24	13	37	44	1553
1991	17	14	64	33	1669
1992	8	3	13	7	1422
1993	15	12	87	16	1372
1994	8	13	48	11	1405
1995	5	3	3	3	1156
1996	23	71	125	176*	1805
1997	9	7	8	30	1608
1998	3	2	12	10	1290
Mean	25	23			1439
SE	4	5			35
CV (%)	78	100			13

Note: WS 3 and WS 6 are untreated reference watersheds and WS 4 and WS 5 are treatment watersheds. WS 4 was progressively strip-cut in 1970–1974. WS 5 was whole-tree clear-cut in 1983–1984. *Significant increase ($p < 0.05$).

[a]Estimated by linear regression with WS 6 as the independent variable.
[b]First set of strips harvested on WS 4.
[c]Second set of strips harvested on WS 4.
[d]Third set of strips harvested on WS 4.
[e]Whole-tree clear-cutting on WS 5.

Stream water nutrient concentrations

Both the SC and the WT caused stream water concentra-

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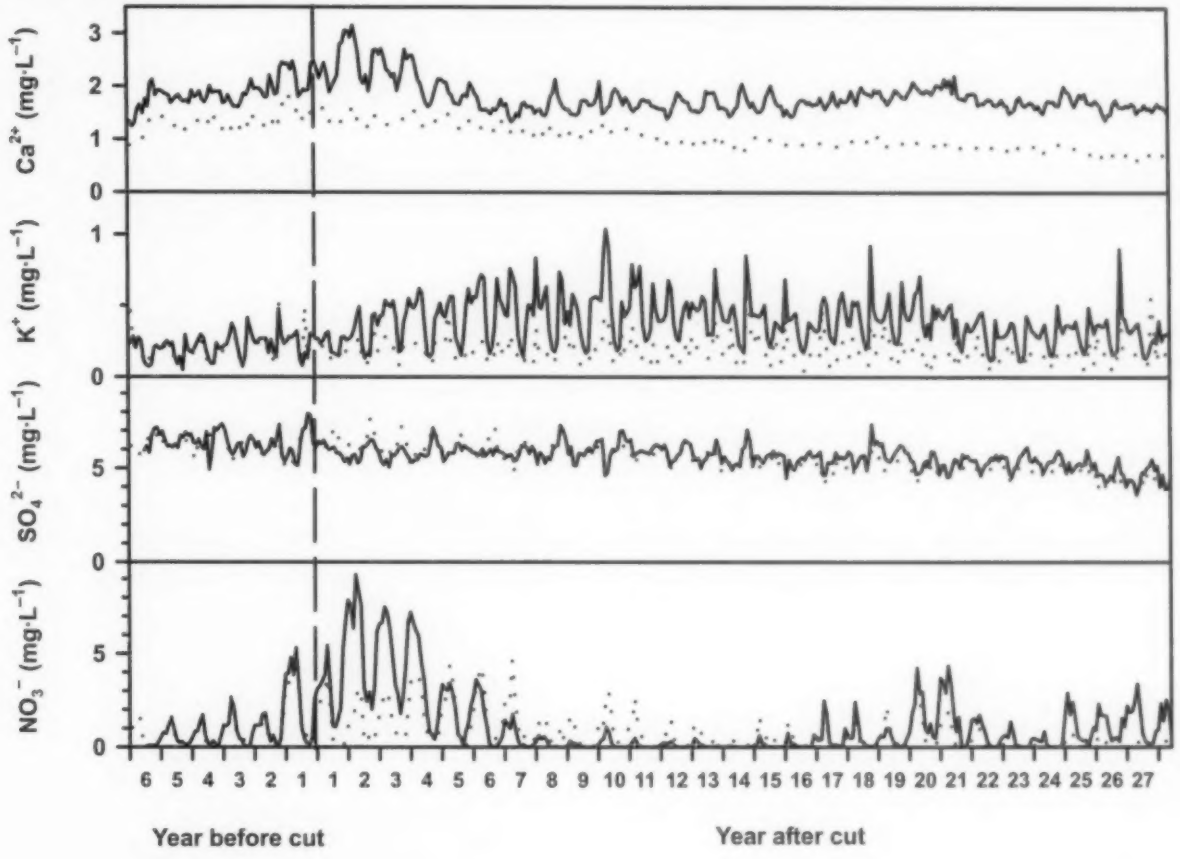
Fig. 1. Volume-weighted mean monthly concentrations of nutrient ions for strip-cut (WS 4) (solid line) and reference (WS 6) (dotted line) watersheds. The vertical dashed line indicates the beginning of the 4-year harvest period. Year 6 before cut is 1964–1965. Year 27 after cut is 1997–1998.



tions of Ca^{2+}, K^+, H^+, and NO_3^- to increase, concentrations of SO_4^{2-} to decrease, and concentrations of other ions to change very little. Before harvest, weighted mean monthly Ca^{2+} concentrations averaged about 2 mg·L^{-1} from the SC and just over 1 mg·L^{-1} from the reference watershed (Fig. 1). The SC caused mean monthly Ca^{2+} concentrations to increase by as much as 0.8 mg·L^{-1} during the 4-year harvest period, but the elevated concentrations returned to preharvest levels, or even a little below, during the fifth through tenth years after initiation of harvest. Ca^{2+} concentrations from the reference watershed have been declining (Likens et al. 1998), but those from the SC have remained fairly uniform at just over 1 mg·L^{-1} (Fig. 1). On the WT, mean monthly Ca^{2+} concentrations increased by as much as 3.5 mg·L^{-1} by the second year after cutting and then gradually declined through year 5 (Fig. 2). During years 5 through 14, Ca^{2+} concentrations from the WT have remained elevated by an average of 0.5 mg·L^{-1} when compared with the reference watershed.

Concentrations of K^+ gradually increased during and immediately after the 4-year period of SC, reaching a maximum increase of 0.6 mg·L^{-1} in year 10 (Fig. 1). Stream water K^+ from the SC has remained elevated through year 27. After the WT, K^+ increased rapidly during the first year, reaching a maximum of 1.5 mg·L^{-1} greater than the reference watershed and then gradually declined over years 2 and 3. As with the SC, elevated levels of K^+ have persisted for the period of measurement (Fig. 2).

Concentrations of H^+ in the stream from the WT increased nearly threefold from precut concentrations during the second and third years after harvest and then declined rapidly to levels below precutting concentrations. Concentrations of H^+ in the stream from the SC increased markedly during the years of the progressive harvest and then rapidly returned to precut concentrations (Fig. 3).

Concentrations of NO_3^- in the reference streams have nearly always been <5 mg·L^{-1} and in recent years have usually been <1 mg·L^{-1} (Figs. 1 and 2). During the 4-year period in which the SC was in progress, volume-weighted mean monthly NO_3^- concentrations were increased by 2–4 mg·L^{-1} (Fig. 1). In year 6, NO_3^- dropped below levels in the reference watershed and remained there through year 15 (Fig. 1). At that point, the pattern reversed, and since then, NO_3^- from the SC has exceeded the values for the reference watershed by as much as 2 mg·L^{-1}. In the first year after WT, mean monthly concentrations of NO_3^- increased from

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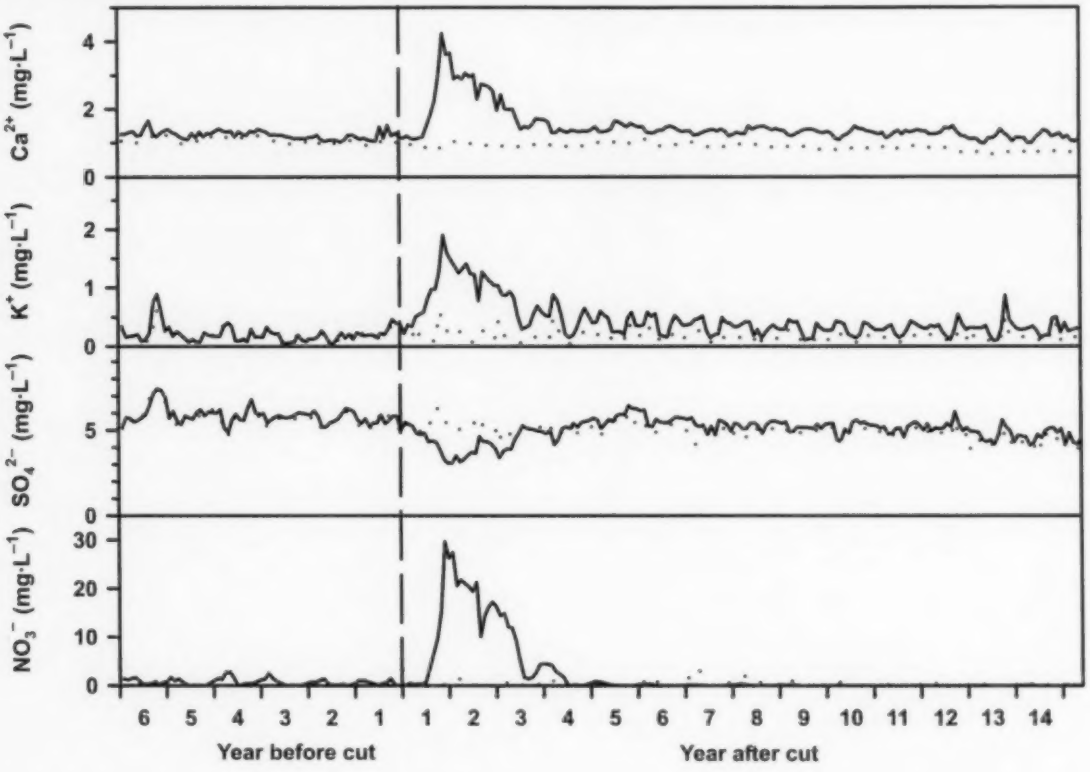
Fig. 2. Volume-weighted mean monthly concentrations of nutrient ions for whole-tree clear-cut (WS 5) (solid line) and reference (WS 6) (dotted line) watersheds. The vertical dashed line indicates the beginning of the harvest. Year 6 before cut is 1978–1979. Year 14 after cut is 1997–1998.



background levels of <1 mg·L^{-1} to a maximum of 30 mg·L^{-1} (Fig. 2). The increases gradually disappeared and concentrations of NO_3^- fell below those for the reference watershed by the sixth year after harvest. The decreased level of NO_3^- from the WT continued through year 14 after harvest.

Concentrations of SO_4^{2-} during preharvest ranged between 5 and 7 mg·L^{-1} and seldom varied between watersheds by more than 0.5 mg·L^{-1} (Figs. 1 and 2). The SC caused mean monthly SO_4^{2-} concentrations to decrease by up to 1.5 mg·L^{-1} during the 4-year harvest interval. After that, SO_4^{2-} returned to preharvest levels. A similar pattern occurred after the WT. Sulfate concentrations decreased by up to 2 mg·L^{-1} during the first 4 years after harvest and then returned to about the same or slightly higher concentrations than from the reference watershed (Fig. 2).

Watershed nutrient budgets

The changes in water yield and ion concentrations for the harvested watersheds caused stream flow nutrient outputs and net gains or losses from input–output budgets to differ from values for uncut reference watersheds. For example, totalling statistically significant increases and decreases in annual stream flow ouputs (Tables 5 and 6) shows that in the 27 years since initiation of SC, there has been an increased loss of 66 kg Ca·ha^{-1}, 62 kg K·ha^{-1}, 33 kg N·ha^{-1}, and 2 kg S·ha^{-1}. Corresponding values for the 14 years following WT are 64 kg Ca·ha^{-1}, 39 kg K·ha^{-1}, 54 kg N·ha^{-1}, and 17 kg S·ha^{-1}.

To put these losses in perspective, stream water outputs of Ca in the absence of SC would have been 368 kg Ca·ha^{-1} (Table 5). The additional 66 kg Ca·ha^{-1} lost due to SC thus represents an increase of 18% in total Ca outputs in stream water during the 27 years. Corresponding increases due to SC for other nutrients are 109% for K, 52% for N, and <1% for S. Corresponding increases for the 14-year period following WT are 54% for Ca, 172% for K, 375% for N, and 9% for S.

Despite the large increase in N loss after WT, the watershed still experienced a small net gain in N for the post-harvest period due to the fact that inputs in bulk precipitation continued to exceed outputs in stream flow (Table 6). Such was not the case for Ca and K. The input–output budgets for both of these nutrients show substantial net losses before harvesting, thus even greater net losses after harvest (Tables 5 and 6).

Discussion

Intensive harvesting has a measurable effect on the forest environment including the associated aquatic ecosystems. Canopy removals affect water yields, sediment loads, and nutrient status of streams, all of which affect aquatic life, in-

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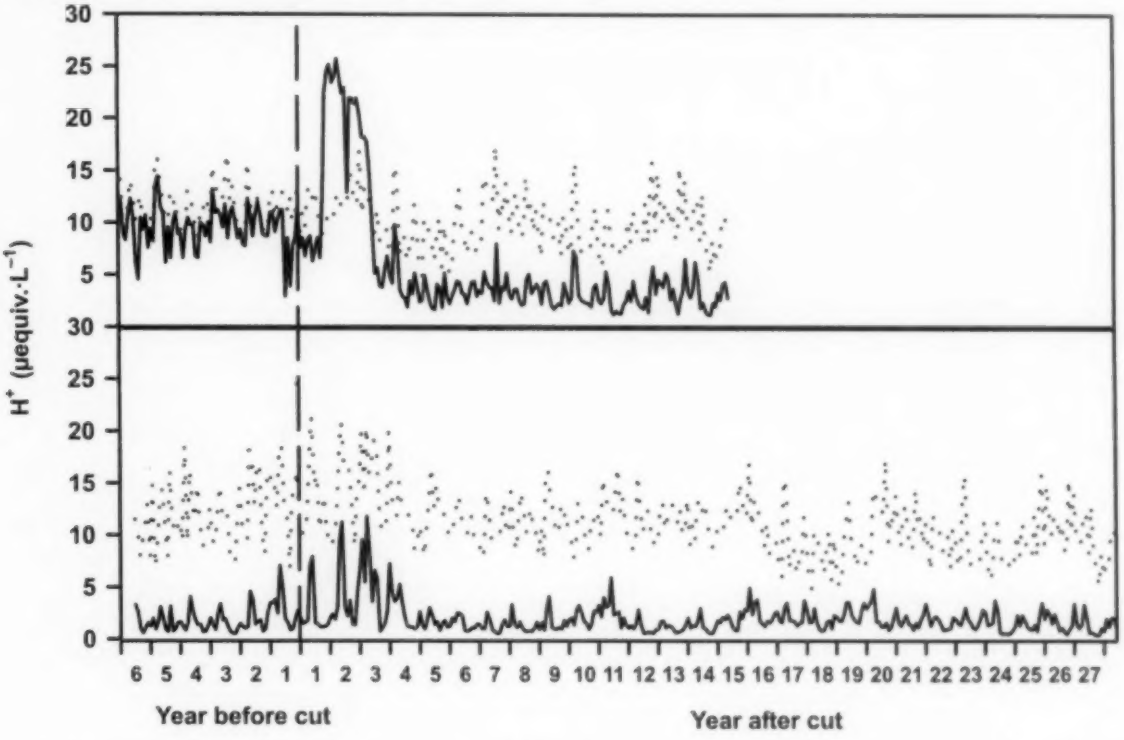
Fig. 3. Volume-weighted mean monthly concentrations of H^+ in stream water from the strip-cut (WS 4) (solid line, bottom panel), whole-tree clear-cut (WS 5) (solid line, top panel), and reference (WS 6) (dotted lines, both panels) watersheds. The vertical dashed line represents the beginning of the harvest period.



cluding fisheries. Below, we discuss the processes at work as the forest ecosystem reorganizes following intensive harvest of northern hardwoods and their effects on aquatic ecosystems.

Impacts of changes in water yield and storm peaks

Increases in water yield immediately after forest harvest occur primarily as augmentation of low flows during summer and early autumn and thus may be beneficial to aquatic ecosystems. Storm peaks may be increased during the growing season, but this effect generally decreases as the size of the storm event increases. Since the magnitude of the increases in peak flows is relatively small (<60%), impacts of harvesting on storm peaks are of minor importance in terms of stream and channel scour, aquatic habitat, and biota. The increases in water yield and storm peaks disappear within only a few years of regrowth and in the case of the SC may even become stream flow decreases. Such decreases in stream flow occur during the growing season and thus have adverse impacts compared with the increases that occur immediately after harvest.

The SC and WT are on small, first- and second-order watersheds. The changes in water yield and storm peaks due to harvest, while of significance in small headwater streams, will quickly be masked as the streams from the harvested watersheds join larger streams. Such is the case for most of the northeastern United States; harvesting is not of sufficient scale to increase downstream flood potential or have measurable impacts on low flow levels. The major concern should be that logging operations and culverts within and immediately downstream of intensively harvested sites are designed and located to accomodate increases in peak flows during the first several years after harvest.

Sediment

Sediment yields from undisturbed northern hardwood forests of New England are among the lowest in North America, averaging about 40 $kg \cdot ha^{-1} \cdot year^{-1}$, but may range as high as 150 $kg \cdot ha^{-1} \cdot year^{-1}$ (Bormann and Likens 1979). Fluctuations in sediment yield from undisturbed forests are not related to watershed size and may vary markedly between watersheds. They are highly variable from year to year and are not well correlated with annual precipitation amounts. High sediment yields are caused by the occurrence of large individual storms (Bormann et al. 1974; Bormann and Likens 1979; Martin and Hornbeck 1994). Sediment yields from harvesting are site and operation specific. The values reported in this paper are from one case study and cannot be expected under other conditions. However, consequences to aquatic systems and fisheries can be minimized if BMPs are followed carefully, even following intensive harvesting with considerable soil disturbance.

Nutrients

Harvesting of northern hardwood forests sets in motion a series of physical and chemical changes. Removal of the for-

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Table 5. Annual input–output budgets (kg·ha^{-1}) for the strip-cut watershed.

	Ca			K			NO_3-N			SO_4-S		
Water year after harvest	Input in precipitation	Output if uncut	Change due to cut	Input in precipitation	Output if uncut	Change due to cut	Input in precipitation	Output if uncut	Change due to cut	Input in precipitation	Output if uncut	Change due to cut
1	1.2	15.6	6.9*	0.3	1.9	1.0*	5.0	4.2	9.0*	11.3	16.1	–1.5*
2	1.1	20.1	6.3*	0.6	2.5	2.0*	5.1	4.6	9.3*	13.1	21.2	–0.9
3	2.0	27.1	8.3*	0.8	3.2	4.8*	7.0	8.1	8.8*	18.0	27.3	1.6
4	1.1	16.4	0.8	0.5	2.3	1.8*	4.7	4.9	0	11.9	17.0	0.7
5	1.2	21.8	1.3	0.3	2.4	4.8*	5.6	6.5	–0.7*	13.6	23.9	2.3*
6	1.3	14.8	–0.7	0.3	2.1	3.8*	5.7	5.0	–2.9*	10.9	16.3	1.9*
7	1.1	15.9	0.2	0.4	2.0	3.8*	5.6	1.9	–1.2*	13.2	18.9	0.6
8	0.8	13.2	–0.1	0.3	2.0	2.5*	5.2	1.6	–1.3*	11.5	16.4	–0.6
9	1.1	12.2	–0.6	0.4	2.3	3.0*	4.6	2.7	–2.1*	9.0	13.7	–0.3
10	1.3	12.9	–0.4	0.5	2.2	2.9*	5.1	2.8	–2.5*	10.5	15.2	0.1
11	1.1	14.7	2.9*	0.6	2.0	3.9*	5.1	1.7	–1.3*	11.4	19.2	2.2*
12	0.9	11.5	1.5	0.7	1.9	2.2*	4.4	1.2	–1.0*	10.4	15.5	–0.2
13	1.1	12.9	3.0*	0.7	2.5	2.5*	3.4	0.5	–0.5	6.9	17.5	0.6
14	1.0	9.5	1.0	0.6	1.7	1.1*	4.7	1.0	–0.8*	9.4	12.6	–0.6
15	0.9	11.9	2.0	0.4	2.1	2.1*	4.3	1.0	–0.5*	8.1	15.8	–0.2
16	0.6	11.4	2.1	0.3	2.3	1.0*	3.7	1.8	0.4*	8.4	14.1	–0.5
17	1.1	10.7	2.3	0.7	1.7	1.9*	4.7	0.9	0.6*	8.6	13.6	–0.3
18	1.1	10.4	1.0	0.5	2.1	1.1*	5.0	1.7	–0.7*	8.5	12.9	–0.8
19	1.4	14.8	5.2*	0.9	2.5	3.1*	5.5	4.2	0.7*	10.2	17.5	–0.8
20	1.2	14.4	7.3*	0.8	1.8	3.0*	5.6	2.0	3.6*	11.6	18.5	0
21	1.1	11.1	4.2*	0.6	1.7	1.5*	4.9	0.7	1.2*	7.2	15.0	–0.2
22	0.9	10.6	3.6*	0.6	1.7	1.1*	5.0	0.5	0.7*	7.4	14.7	0.2
23	1.2	10.9	3.3*	0.6	1.6	1.3*	5.9	0.3	0.7*	8.7	15.4	–0.2
24	1.0	8.4	2.3	0.6	1.3	0.7*	4.8	0.5	1.7*	7.1	11.1	1.2
25	1.3	14.1	7.5*	0.7	2.7	2.3*	5.8	0.8	3.4*	8.6	20.4	0.6
26	1.1	11.6	7.0*	0.6	2.1	2.1*	5.3	0.5	4.9*	7.8	16.9	–0.9*
27	1.1	8.6	2.6	0.8	1.7	0.3*	4.4	0.4	2.5*	6.6	11.7	–1.8*
Sum	30.3	367.5	65.5[a]	15.1	56.3	61.6[a]	136.1	62.0	32.5[a]	269.9	448.4	2.2[a]

Note: *Significant at the 0.05 level of probability.
[a]Sum of significant differences only.

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Table 6. Annual input–output budgets ($kg \cdot ha^{-1}$) for the whole-tree clear-cut watershed.

	Ca			K			NO_3-N			SO_4-S		
Water year after harvest	Input in precipitation	Output if uncut	Change due to cut	Input in precipitation	Output if uncut	Change due to cut	Input in precipitation	Output if uncut	Change due to cut	Input in precipitation	Output if uncut	Change due to cut
1	1.0	7.0	14.0*	0.6	1.5	8.2*	4.5	0.9	28.3*	9.2	11.1	–1.1
2	0.9	8.9	12.3*	0.4	1.7	7.6*	4.2	0.9	28.8*	7.9	14.6	–2.3
3	0.6	8.5	2.9*	0.3	2.0	3.2*	3.6	1.6	3.5*	8.3	12.7	–0.3
4	1.1	7.9	1.9*	0.7	1.4	2.0*	4.6	0.8	–0.3	8.3	12.2	0.9*
5	1.1	7.6	1.8*	0.5	1.8	1.7*	4.8	1.5	–1.3*	8.3	11.4	1.5*
6	1.4	11.1	3.0*	0.8	2.2	2.4*	5.4	3.8	–3.7*	10.1	16.5	3.1*
7	1.2	10.8	4.2*	0.8	1.5	2.5*	5.6	1.9	–1.6*	11.6	17.6	1.8*
8	1.1	8.2	3.8*	0.6	1.4	1.7*	4.8	0.6	–0.4	8.9	13.7	1.9*
9	0.9	7.8	3.2*	0.6	1.4	1.7*	5.0	0.4	–0.3	9.0	13.4	1.2*
10	1.2	8.1	3.1*	0.6	1.4	1.6*	5.8	0.2	–0.2	10.0	14.2	1.0*
11	0.9	6.1	2.1*	0.6	1.0	1.1*	4.8	0.4	–0.4	7.8	9.5	1.2*
12	1.3	10.6	4.9*	0.7	2.3	2.5*	5.8	0.7	–0.6	9.0	19.6	2.6*
13	1.1	8.6	4.5*	0.6	1.8	2.2*	5.3	0.4	–0.2	8.9	15.8	2.2*
14	1.0	6.3	2.0*	0.8	1.4	0.9*	4.4	0.3	–0.2	6.7	10.2	0.9
Sum	14.8	117.5	63.7[a]	8.6	22.8	39.3[a]	68.6	14.4	54.0[a]	124.0	192.5	17.4[a]

Note: *Significant at the 0.05 level of probability.
[a]Sum of significant differences only.

est canopy exposes the forest floor to incident solar radiation that greatly warms the organic horizons (Likens et al. 1970; Hornbeck et al. 1986). Removal of the canopy also reduces transpiration and increases soil moisture. This warm, moist environment is conducive to a dramatic increase in the populations of soil microorganisms (Bormann and Likens 1979; Dahlgren and Driscoll 1994). The combined increase in light, heat, moisture, and soil organisms results in increased rates of organic matter decomposition and soil mineralization (Bormann and Likens 1979; Hornbeck et al. 1986; Johnson 1995), which in turn leads to significant nitrification and production of nitric acid in both the forest floor and the mineral soil (Likens et al. 1970; Bormann and Likens 1979; Dahlgren and Driscoll 1994). Nitric acid production acidifies the soil by cation exchange and mobilizes base cations (Ca^{2+}, Mg^{2+}, Na^{+}, and K^{+}) and Al^{3+}. Base cations bind with NO_3^- and leach from soils to stream water (Likens et al. 1970; Dahlgren and Driscoll 1994).

The NO_3^- losses over the 4 years following harvest are of interest. Covington (1981) and Federer (1983) predicted that by year 8 after heavy cutting, 25–40% of the N in the forest floor would be lost. However, work on the WT indicated that only 17% of the forest floor N had been lost by year 8 (Johnson 1995). The redistribution of organic matter from the forest floor to lower soil horizons during the harvesting process was suggested as contributing to the reduction in N loss, since it was not lost but moved to lower horizons. Furthermore, regeneration and renewed uptake of N were rapid on the WT (Mou et al. 1993). NO_3^- is highly mobile in soil solution and leaches readily from soils to streams. However, it is readily taken up by regeneration and incorporated into plant tissue (Bormann and Likens 1979; Dahlgren and Driscoll 1994), a process that apparently limited N loss from the WT and contibuted to the rapid decline of stream NO_3^- levels by year 4.

Stream nutrient concentrations did not peak until a full year after harvest began on the WT. Dahlgren and Driscoll (1994) attributed this to a high C:N ratio at the time of harvest. With the change in physical conditions after harvesting leading to rapid organic matter decomposition and nitrification, the C:N ratio declined. As the C:N ratio declined, microbial demands, decomposition, and leaching declined with them. Johnson (1995) found that more C was lost from the soils of the whole-tree harvest than N, thus lowering the C:N ratio. The N to organic matter ratio did not change after cutting. Thus, rapid regeneration of the harvested sites is the key to minimizing organic matter and N losses from harvests (Bormann and Likens 1979; Johnson 1995; Pardo et al. 1995).

Unlike other ions, SO_4^{2-} in stream water declined immediately following harvesting. Nitrification and mineralization of N release H^+, which acidifies the forest soil and soil water and in so doing increases the SO_4^{2-} adsorption capacity of the soil (Nodvin et al. 1986; Mitchell et al. 1989). On the WT, Mitchell et al. (1989) found that SO_4^{2-} adsorbed in the E and Bh horizons during the first 2 years after cutting accounted for 88% of the decline in stream water SO_4^{2-} concentrations. Organic S released during decomposition was deposited in the B horizons. The net effect was that there was only a 9% change in total S leaving the watershed as a result of the harvest.

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The harvest had a measurable effect on stream chemistry during the first 3 years after harvest. During this period, increases in stream flow, light, temperature, and nutrients translated into increased algal abundance with little change in species composition or diversity (Ulrich et al. 1993). The increase in the algal abundance in turn affected the macroinvertebrate community. The standing crop of invertebrates increased the first growing season after cutting due to an increase in herbivorous forms (Burton and Ulrich 1994). At the same time, the populations of two predatory invertebrates also increased. These increases were at the expense of the leaf-shredding detritivores. In summary, the whole-tree clear-cutting reduced the species diversity of invertebrates but increased the abundance (Burton and Ulrich 1994).

Acidification of the soils and streams associated with nitrification and NO_3^- production during the first 3 years after harvesting also released inorganic Al from the soils to the streams (Lawrence et al. 1987). The Al levels in soil solutions and streams in the WT were greater than those found in a stream acidification manipulation at HBEF (Hall et al. 1980) and have the potential to impact aquatic life (Lawrence et al. 1987). Research at other locations has reported Al levels lower than those resulting after the WT to be toxic to fish (Lawrence et al. 1987). While these potentially toxic levels of Al did abate as nitirification declined and stream water became less acidic than before harvesting, the effects of elevated concentrations of inorganic Al in the streams during the first 3 years after harvest extended downstream from the harvest (Lawrence and Driscoll 1988).

While the processes at work in the SC seemed to be the same as from the WT, the magnitudes of the effects were greatly reduced by the progressive nature of the SC. Although both watersheds were eventually clear-cut, NO_3^- concentrations from the SC were only one third those of the WT and net N losses were less than half. The rapid regeneration and vegetation in the uncut buffer strips consumed available NO_3^- to the point where from years 7 through at least year 14 on both watersheds, stream water NO_3^- concentrations were less than precutting levels. The surprising results are that K^+ and Ca^{2+} concentrations have not returned to precutting levels through year 27. Furthermore, by year 20 on the SC, NO_3^- concentrations and net losses again have risen significantly above reference levels. This result may be attributed to the loss of pin cherry from the regeneration (Hornbeck et al. 1997) or to the fact that the regenerating forest does not yet fully occupy the rooting zone of the preharvest forest. Pin cherry colonized both these watersheds in copious numbers. It is a short-lived pioneer species that begins to drop from the forest composition by year 20 to almost completely disappear by year 35 (Marks 1974; Bormann and Likens 1979) and is replaced by more shade-tolerant species that compose the mature forest. This radical change in stand composition and the rapid decomposition of pin cherry biomass on the forest floor may explain increased NO_3^- in the streams.

The combination of rapid regeneration after harvest and the careful application of BMPs help to keep harvest-induced changes in nutrient concentrations and subsequent nutrient outputs to low levels. Outputs of nutrients and sediment in streams have implications with regard to programs being initiated to improve water quality and protect aquatic habitat. Section 303(d) of the United States Clean Water Act establishes total maximum daily loading (TMDL) as a process for controlling pollution from both point and nonpoint sources. The TMDL is defined as a calculation of the maximum amount or loading of a pollutant that a water body can receive and still meet water quality standards. Results from our study provide indications of loading that can be anticipated from cut and uncut forests, both of which are presently considered nonpoint sources.

Normal, background loading of streams from uncut forests averaged around 8, 2, and 1 $kg \cdot ha^{-1} \cdot year^{-1}$, respectively, for Ca^{2+}, K^+, and NO_3-N. For the first year after WT, loading was increased twofold for Ca^{2+}, fivefold for K^+, and 30-fold for NO_3-N. The increases declined quickly with forest regrowth and were less than twofold for all nutrients by the fourth year after WT. Findings such as these may be useful in the TMDL process to help develop standards and guides for streams and watersheds subjected to various uses and sources of pollution.

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Stream temperature responses to forest harvest and debris flows in western Cascades, Oregon

Sherri L. Johnson and Julia A. Jones

Abstract: Stream temperature controls the rates of many biotic and abiotic processes and is influenced by changes in streamside land use practices. We compiled historic stream temperature data and reestablished study sites in three small basins in the H.J. Andrews Experimental Forest in the western Cascades, Oregon, to reexamine the effects on and recovery of stream temperatures following removal of riparian vegetation. Maximum stream temperatures increased 7°C and occurred earlier in the summer after clear-cutting and burning in one basin and after debris flows and patch-cutting in another. Diurnal fluctuations in June increased from approximately 2 to 8°C. Stream temperatures in both basins gradually returned to preharvest levels after 15 years. The influence of the primary factor controlling stream temperatures, shortwave solar radiation, was amplified following removal of riparian vegetation, and conduction between stream water and nearby soils or substrates also appeared to be an important factor. Shifts in the timing of summer maxima and greater increases in early summer stream temperatures could impact sensitive stages of aquatic biota.

Résumé : La température des cours d'eau régit le rythme de nombreux processus biotiques et abiotiques, et se trouve sous l'influence des changements dans les pratiques d'aménagement du territoire sur les rives. Nous avons compilé les données historiques sur la température des cours d'eau et rétabli des stations d'étude dans trois petits bassins de la forêt expérimentale H.J. Andrews, dans l'ouest des Cascades (Oregon), pour réexaminer les effets de l'enlèvement de la végétation riveraine sur la température des cours d'eau, et le rétablissement subséquent. Les températures maximales des cours d'eau ont augmenté de 7°C, et les augmentations se sont produites plus tôt dans l'été, après la coupe à blanc et le brûlage dans un bassin, et après des apports de débris et du jardinage par bouquets dans un autre. Les fluctuations diurnes en juin ont augmenté d'environ 2 à 8°C. Dans les deux bassins, les températures des cours d'eau sont graduellement revenues aux niveaux pré-exploitation au bout de 15 ans. L'influence du principal facteur régissant la température des cours d'eau, le rayonnement solaire à ondes courtes, a été amplifiée par suite de l'élimination de la végétation riveraine, et la conduction entre l'eau de la rivière et les sols ou les substrats adjacents semblait aussi un facteur important. Les changements dans l'occurrence des maximums d'été, et les augmentations plus fortes des températures des cours d'eau au début de l'été, pourraient avoir un impact sur les stades vulnérables du biote aquatique.

[Traduit par la Rédaction]

Introduction

Stream temperature is a critical parameter in stream ecosystems. Temperature controls rates of metabolism, growth, decomposition, and solubility of gases as well as many processes and biotic interactions (Beitinger and Fitzpatrick 1979; Beschta et al. 1987). As a consequence, increases in stream temperature in regions with cold-water fisheries have been linked to potential fish mortality (Brett 1952; Beschta et al. 1987), increased prevalence of disease (Becker and Fugihara 1978), and changes in interspecific competition (Reeves et al. 1987; Ward and Stanford 1992).

Temporal and spatial variations in stream temperature are the result of multiple factors that interact with one another (Brown 1969). Direct solar radiation on the water surface is a dominant source of heat energy for streams (e.g., Beschta et al. 1987; Sinokrot and Stefan 1993; Webb and Zhang 1997), but other sources and fluxes of energy also contribute to stream temperature at a given point (Fig. 1). These include energy exchange by conduction between stream water and the stream substrata (Crittenden 1978; Hondzo and Stefan 1994; Evans et al. 1995), evaporation and sensible heat exchange with the atmosphere (Sinokrot and Stefan 1993; Webb and Zhang 1997), and energy contributed by advection of water from deep groundwater sources and upstream (Ingebritsen et al. 1992; Webb and Zhang 1997).

Forest harvest in riparian areas has been shown to produce increases in stream temperatures, and the magnitude of these increases varies among sites and regions (Swift and Messer 1971; Anderson 1973; Beschta et al. 1987). Sites where only overstory riparian vegetation was removed generally had smaller increases in stream temperature than where the understory was also removed through burning or herbicide treatments (Levno and Rothacher 1969; Lynch et al. 1984). Responses among sites also varied as a function of the amount of stream surface exposed by harvesting. Most studies of forest harvest effects have been limited to a few post-harvest years (summarized by Anderson 1973; Beschta et al.

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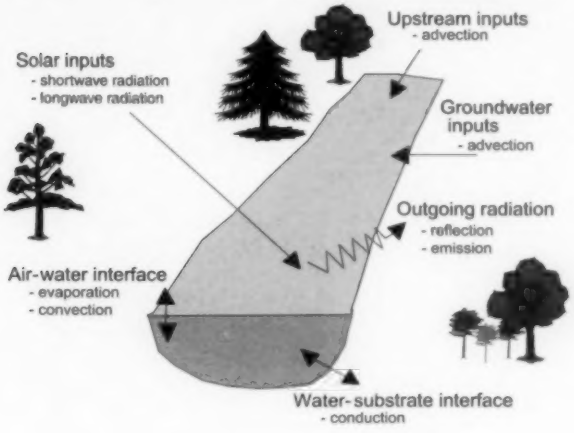
Fig. 1. Factors and mechanisms influencing stream temperature.



1987), and in other studies, the lack of pretreatment data has precluded documentation of stream temperature recovery to preharvest levels (Hostetler 1991). Although, to our knowledge, long-term responses of stream temperature have not been examined, except by Moring (1975), trends of diminishing stream temperatures with forest recovery have been observed or predicted (e.g., Brown and Krygier 1970; Swift 1982; Beschta and Taylor 1988).

Forest harvest and debris flows in small experimental basins in the H.J. Andrews Experimental Forest, western Cascades, Oregon, during the 1960s led to elevated stream temperatures in the years immediately following harvest (Levno and Rothacher 1967, 1969). Continued monitoring of stream temperatures, discharge, vegetation dynamics, and climate allows us to examine the long-term recovery of stream temperatures following forest harvest. Here, we examine (*i*) major mechanisms controlling stream temperatures, (*ii*) effects of riparian vegetation removal and recovery on summer stream temperatures, and (*iii*) changes in the timing of summer maximum stream temperatures following riparian vegetation removal.

Materials and methods

Study site

This study was conducted in three small (<1 km^2) basins in the H.J. Andrews Experimental Forest (Fig. 2). The climate in the lower elevations of the western Cascade Mountains is considered xeric with warm dry summers and cool to cold rainy winters. Mean annual precipitation is 2.4 m, most of which occurs between November and April. Very little rain falls during summer, and stream flows generally decline from June through August (Fig. 3). Stream channels are steep and confined, with unsorted sediment ranging in size from boulders to silt and with large wood and exposed bedrock in some locations.

Prior to harvest, native vegetation in these small basins was 450-year-old forest dominated by Douglas-fir (*Pseudotsuga menziesii*). Stream flow and other basin characteristics (Table 1) have been monitored since 1952 as part of a paired-basin experiment to examine the effects of forest harvest on stream flow and vegetation. Results of this experiment have been described in other studies (e.g., Dyrness 1973; Jones and Grant 1996).

Forest harvest history differs among the three basins. Watershed 2 (WS 2) is an unharvested, unroaded basin with old-growth vegetation. Watershed 1 (WS 1) was 100% clear-cut between 1962 and 1966, but no roads were constructed. Trees, including those in riparian zone, were removed using cable-logging methods, logging slash was broadcast burned in September 1966, and some wood was removed from the channel (Levno and Rothacher 1969). In watershed 3 (WS 3), 2.6 km of roads were constructed between 1959 and 1961, and in 1963, 25% of the basin was harvested in three "patch cuts," which were then broadcast burned. In December 1964, debris flows scoured upstream sections of the channel to bedrock, removed all riparian vegetation, and deposited sediment and wood in the lower section (Levno and Rothacher 1967).

After harvest, herbaceous and shrub vegetation on hillslopes established rapidly, reaching preharvest levels of cover within 5 years and continuing to increase to twice the preharvest cover conditions over the next 10–20 years in both WS 1 and WS 3 (Halpern and Spies 1995). However, tree cover on hillslopes reestablished more slowly, with less than 10% cover after 5 years, 25% cover after 15 years, and 80–90% cover 30 years after harvest (Halpern and Spies 1995). In the riparian zone in WS 1, a dense stand of red alder (*Alnus rubra*) developed, creating canopy closure approximately 15 years after harvest. Alder stand development along the stream channel of WS 3 was less vigorous and limited by bedrock outcrops (F. Swanson, U.S. Forest Service, Forestry Sciences Laboratory, 3200 SW Jefferson Way, Corvallis OR 97331, U.S.A., personal observation). Riparian vegetation in WS 3 was removed by debris flows in February 1996 that again scoured the upper 1 km of channel and deposited sediment and large wood in the lower 200-m reach (Swanson et al. 1998).

Data acquisition

Stream temperature, discharge, air temperature, precipitation, solar radiation, and soil temperatures have been monitored over varying periods, with increased temporal resolution in the later years (Table 1). Stream temperature was monitored just above the stream gauging stations (Fig. 2). Precipitation and air temperature data were collected at the WS 2 climate station (C, Fig. 2), while solar radiation and soil temperature data were collected at the primary climate station (P, Fig. 2). Additional soil temperature data were collected in the WS 2 reference stand (R, Fig. 2). For the summer of 1967, when no solar radiation sensors were in place, solar radiation was modeled based on a multiple regression for the period 1979–1991, which estimated solar radiation as a function of solar angle, precipitation, and air temperature (Forest Science Data Bank, Corvallis, OR 97331, U.S.A.). Stream temperature data were suited for analysis at several temporal scales: (*i*) the 23-year record of summer maximum temperatures from 1959 to 1982, (*ii*) the 6-year record of weekly maximum and minimum temperatures from the summers of 1960, 1967–1970, and 1997, (*iii*) daily maximum and minimum summer temperatures in 1967 and 1997, and (*iv*) hourly summer stream temperatures in 1967 and 1997. Prior to 1997, stream temperatures were measured in degrees Fahrenheit to the nearest whole number. We converted all values to Celsius and report stream temperatures to the nearest 0.1°C, recognizing that slight differences in historic values would not have been detectable at this level of precision.

Statistical analysis

Statistical analyses were conducted to compare mean weekly maximum and minimum stream temperatures among years and months in WS 1, WS 2, and WS 3. Because daily stream temperatures are autocorrelated, and preharvest maximum and minimum stream temperatures had been collected at weekly time steps, the daily data from 1967 to 1970 and from 1997 were subsampled to obtain maximum and minimum stream temperatures for approxi-

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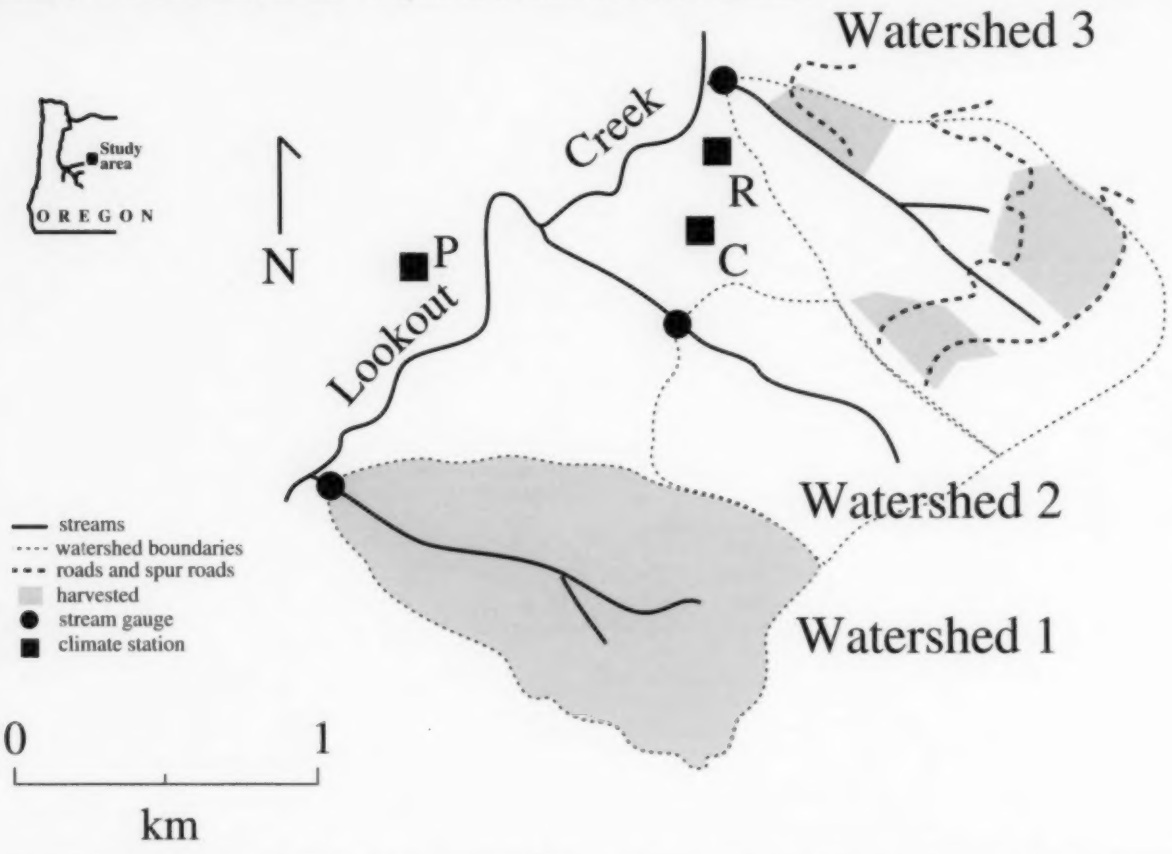
Fig. 2. Location of experimental basins in the H.J. Andrews Experimental Forest, western Cascades, Oregon. WS 1 was clear-cut and burned, WS 2 was unharvested, and WS 3 was patch-cut but debris flows scoured the channel.



mately weekly intervals (ranging from 5 to 8 days) corresponding to those sampled in 1960. Hence, data consisted of 17 observations per summer of weekly maximum (minimum) stream temperatures, with four observations for June, four for July, five for August, and four for September. Statistical analyses were conducted using complete factorial analysis of variance (ANOVA) with post hoc tests using multiple comparisons (Neter et al. 1990). Interannual variation in stream temperatures from the unharvested basin (WS 2) was examined using weekly maximum or minimum stream temperature as the dependent variable and year and month as the independent variables. Interannual and monthly changes associated with clear-cutting or patch-cutting and debris flows were analysed using differences between harvested and unharvested basins. The dependent variable in these analyses was the difference between the maximum (or minimum) weekly stream temperatures in the harvested basins (WS 1 or WS 3) and the unharvested basin (WS 2); year and month were the independent variables. Post hoc tests of effects were conducted to identify significant differences. Because multiple years and months were compared, probabilities were conservatively adjusted using Tukey's highest significant difference test to guarantee an overall protection of $\alpha = 0.05$ (Neter et al. 1990; SPSS, Inc. 1998).

Results

Interannual and seasonal variability

In the unharvested basin, WS 2, summer temperatures varied among years and among months. Maximum summer temperatures ranged from 15 to 19°C, with a mean of 16.7°C from 1959 to 1982 (Fig. 4). In WS 2, mean weekly maximum stream temperatures were not significantly different among the six years (1960, 1967–1970, and 1997) ($F = 1.7$, $p = 0.129$) but were significantly higher in July and August than in June or September ($F = 19.1$, $p < 0.001$). Mean weekly minimum stream temperatures were significantly higher in 1967 than in 1960 (Table 2).

Despite differences in disturbances (timing and extent of forest harvest treatment and debris flows), maximum summer temperatures WS 1 and WS 3 had very similar trajectories from 1966 to 1982 (Fig. 4). In WS 1, summer maximum temperature increased to 23.9°C in 1967 and 1968, after clear-cutting and burning, and returned to preharvest levels by the early 1980s. In WS 3 in 1965, 2 years after patch-cutting and 6 months after debris flows, the maximum stream temperature increased to 21.7°C, and in 1968, the summer maximum stream temperature reached 23.9°C.

Weekly maximum stream temperature differences between WS 1 and WS 2 increased significantly during the first several summers after clear-cutting and burning ($F = 285.1$, $p < 0.001$) (Table 3). Differences in weekly minimum stream temperatures also increased in the first summers after harvest ($F = 33.2$, $p < 0.001$). Prior to harvest and again 30

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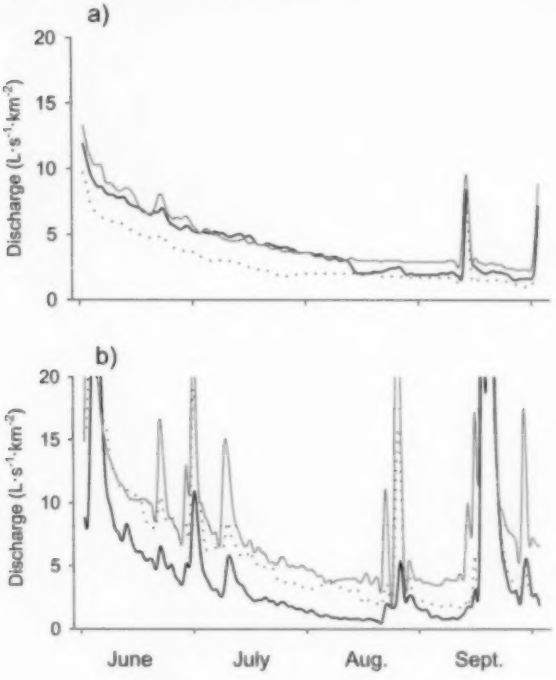
Fig. 3. Mean daily stream discharge measured at the stream gauging weirs in WS 1 (black line), WS 2 (dotted line), and WS 3 (grey line) during (*a*) 1967 and (*b*) 1997.



years after harvest, mean weekly maximum and minimum temperatures differed by less than 1°C (Table 3). In the first 4 years after clear-cutting, mean maximum weekly stream temperatures for the summer were 5.4–6.4°C higher in WS 1 than in WS 2, and mean minimum weekly stream temperatures were 1.6–2.0°C higher in WS 1 than in WS 2 (Table 3). Mean weekly maximum stream temperature differences in June and July were significantly greater than in September ($F = 3.6$, $p < 0.001$). After clear-cutting and burning, maximum stream temperature in June increased to 23.3°C and in July to 23.9°C. In September, maximum temperature was 20.1°C.

Weekly maximum stream temperature differences between WS 3 and WS 2 increased significantly after patch-cutting combined with debris flows ($F = 186.6$, $p < 0.001$) (Table 3). Mean weekly minimum temperature differences increased in 1967 ($F = 11.1$, $p < 0.001$). Prior to harvest and debris flows, weekly maximum and minimum stream temperatures in WS 3 and WS 2 differed by less than 1.1°C; WS 3 had slightly lower maxima and higher minima than WS 2 (Table 3). In 1967–1969, mean weekly maximum stream temperatures for the summer were 3.5–5.2°C higher in WS 3 than in WS 2 and significantly different ($p < 0.001$) from those in 1960 (Table 3). Mean weekly maximum stream temperature differences were larger in June and July than in September ($F = 4.9$, $p < 0.001$). In 1997, stream temperatures in WS 3 reflected the recent channel disturbance by debris flows. Mean weekly maximum stream temperature differences from WS 2 were more than 2.0°C higher than in 1960 ($p < 0.05$) but less than in 1967–1969, after the 1964 debris flow (Table 3). Mean weekly minimum stream temperatures in 1997 were 1.5°C higher in WS 3 than in WS 2 and significantly different ($p < 0.01$) from those in 1960.

Stream temperatures in the unshaded streams (WS 1 and WS 3) responded more dramatically to solar inputs than temperatures in the unharvested basin (WS 2). Differences in daily maximum stream temperatures between WS 1 and WS 2 and between WS 3 and WS 2 were amplified during periods of high solar inputs and reduced during periods of cloud cover in 1967 (Figs. 5*c* and 5*d*). Differences between daily maximum stream temperature in harvested and unharvested basins (WS 1 and WS 2 or WS 3 and WS 2) were greatest in late June and early July and decreased through the summer (Fig. 5*c*).

Diurnal and hourly variability

Stream temperatures in the unshaded streams had wider diurnal fluctuations than in the unharvested basin. In 1967, the maximum diurnal range of stream temperatures was 6–8°C in WS 1 and 5–6°C in WS 3 but only 1–2°C in WS 2 (Figs. 5*a* and 5*b*). By 1997, the diurnal range of stream temperatures was 1–2°C in all three basins (Figs. 6*a* and 6*b*). The timing of daily maxima also changed following clear-cutting in WS 1. In mid-July 1967, daily maximum stream temperatures occurred at 13:00, 6 h earlier than in the old-growth unharvested basin, where stream temperatures peaked at 19:00. Daily minimum stream temperatures occurred at 05:00 in WS 1, whereas in WS 2, they occurred at 08:30. In 1997 in both WS 1 and WS 2, daily maxima occurred between 18:30 and 19:30 and minima occurred at 08:00.

Based on daily mean stream temperatures starting on June 1, degree-days accumulated more rapidly in the clear-cut basin and the basin affected by debris flows than in the unharvested basin. In WS 1 in 1967, 1000 degree-days had accumulated by July 29, 2 weeks earlier than in WS 2 (Fig. 7*a*), whereas in 1997, degree-days accumulated at similar rates in both basins (Fig. 7*b*). In WS 3 in 1967, 1000 degree-days had accumulated 10 days earlier than in WS 2 and 8 days earlier in 1997 (Fig. 7).

Soil temperatures

Diurnal temperature fluctuations in shaded versus unshaded streams were quite similar to soil temperature fluctuations in an old-growth forest stand versus a forest gap (Figs. 5 and 8). In a forest gap, surface soil temperatures (10 cm depth) showed wide diurnal fluctuations and reached summer maxima exceeding 25°C (Fig. 8*a*). Under forest canopy in an old-growth forest stand, surface soil temperatures had narrower diurnal fluctuations and were generally 5°C cooler than temperatures in forest gaps (Fig. 8*b*). Soil temperatures at depth at both sites were cooler than at the surface, had reduced diurnal fluctuations, and were temporally lagged; maximum values at 100 cm occurred in early September, whereas those nearer the surface occurred in mid-August (Fig. 8*a*). In the old-growth forest, stream temperatures were slightly lower than soil temperatures at 30 cm; temperatures in the stream and at 30 cm reached maximum values in mid-August.

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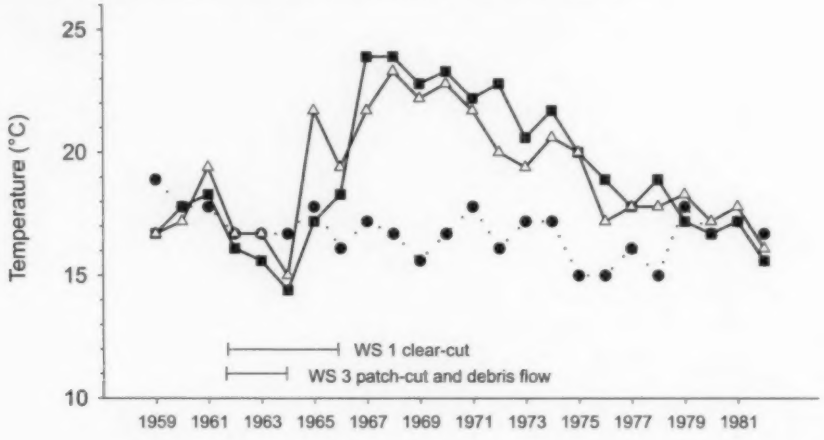
Table 1. Locations, devices, and extent and resolution of data records used in this study.

Variable	Location	Device	Extent of record	Resolution
Stream temperature	WS 1, WS 2, WS 3 stream gauges	"U" tube max.–min. thermometers	1959–1966 (summers)	Weekly max.–min.
	WS 1, WS 2, WS 3 stream gauges	Transducer thermometers and punch tape recorders	1967–1982	Hourly*
	WS 1, WS 2, WS 3 stream gauges	Optic Stowaways	1997–present	30 min
Stream discharge	WS 1, WS 2, WS 3 stream gauges	Stevens A-35 recorder	1952–present	Hourly
Air temperature	WS 2 climate station	Hi-Q hygrothermograph	1958–present	Daily max.–min.
Precipitation	WS 2 climate station	Universal recording rain gauge	1957–present	Daily
Solar radiation	Primary climate station	Pyranometer with thermopyle sensor, data logger	1972–present	Hourly
Soil temperature	Primary climate station at 10, 20, 50, 100 cm	Thermistor probes and data logger	1994–present	Dourly
Soil temperature	WS 2 reference stand	Thermistor probes at 10, 20, 30 cm	1987–present	Daily max.–min.

*Only summer maximums are available from 1971 to 1982.

Fig. 4. Maximum summer season stream temperature (June 1 – September 30) from 1959 through 1982. WS 1(squares) was clear-cut between 1962 and 1966 and then slash burned. WS 2 (circles) was unharvested. WS 3 (triangles) had roads constructed between 1959 and 1961, was patch-cut during 1962–1963, and had debris flows scour the channel in 1964.



Discussion

Stream temperature responses to removal of riparian vegetation occurred at multiple temporal scales, including increases in maximum and minimum daily, weekly, and summer stream temperatures, increased diurnal fluctuations, and shifts in the timing of stream temperature maxima to earlier in the summer season and on a given day. The magnitude and timing of temperature changes are a result of the multiple mechanisms that interact to control stream temperature dynamics.

Physical controls

This study highlighted the importance of solar radiation as a primary driver of stream temperatures and the increased influence of radiation when riparian vegetation was removed, either by clear-cutting and burning or by debris flows. The direct mechanism by which solar radiation warms exposed stream water and soils is radiative exchange (Brown 1969; Monteith and Unsworth 1980). In this study and in others (Brown and Krygier 1970; Holtby 1988), the largest increases in stream temperature after riparian removal occurred not at the usual time of maximum stream temperatures, but in early summer, which coincided with the timing of maximum solar inputs. The shift in timing of increased temperatures was not readily discernable in the daily maximum–minimum temperature records but became apparent in the differences between maximum daily temperatures in shaded and unshaded streams. This pattern of differences between daily maxima parallels the daily magnitude of summer solar radiation that was able to penetrate to the stream surfaces in WS 1 and WS 3 when riparian vegetation had been removed.

Conduction between water and alluvial substrates is often underestimated as an important mechanism influencing stream temperature (Brown 1969; Beschta et al. 1987), and

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Table 2. Average summer conditions (June 1 – September 30) in the unharvested basin, WS 2, during the years indicated.

	Stream temperature (°C)		Air temperature (°C)		Mean daily precipitation (mm)	Mean daily Q ($L \cdot s^{-1} \cdot km^{-2}$)
	Mean max.	Mean min.	Mean max.	Mean min.		
1960	15.2 *a*	10.3 *a*	26.0	9.6	1.0	7.5
1967	15.2 *a*	12.3 *b*	28.9	10.7	0.8	2.8
1968	14.1 *a*	11.1 *ab*	24.2	10.5	2.7	5.8
1969	14.2 *a*	11.2 *ab*	25.5	9.9	1.8	7.2
1970	14.5 *a*	10.8 *ab*	26.4	9.4	1.0	4.3
1997	14.6 *a*	11.7 *ab*	23.3	10.3	2.3	6.0

Note: Stream temperatures are averages of weekly maxima or minima. Air temperatures are the averages of daily maxima or minima. Precipitation is the average of daily totals for the summer. Discharge (Q) is the average of daily means. Stream temperatures were compared among years using ANOVA; values within a column followed by the same letter are not significantly different (Tukey's highest significant difference test, $p < 0.05$).

Table 3. Average differences in weekly maximum or minimum stream temperatures between basins.

		WS 1 and WS 2		WS 3 and WS 2	
	n	Maximum	Minimum	Maximum	Minimum
1960	17	–0.8 *a*	0.5 *a*	–1.1 *a*	0.4 *a*
1967	17	5.8 *b*	2.0 *b*	3.5 *b*	1.0 *b*
1968	17	6.2 *b*	2.0 *b*	5.2 *c*	–0.1 *a*
1969	17	6.4 *b*	1.8 *b*	5.1 *c*	0.1 *a*
1970	17	5.4 *b*	1.8 *b*	—	—
1997	17	–0.4 *a*	0.1 *a*	1.6 *d*	1.5 *b*

Note: The weekly maxima or minima in the unharvested basin (WS 2) were subtracted from those of the clear-cut basin (WS 1) or of the basin with patch cuts and debris flows (WS 3). Data were not available for WS 3 in 1970. Differences were compared among years using ANOVA; values within a column followed by the same letter are not significantly different (Tukey's highest significant difference test, $p < 0.05$).

we suggest that, in reaches without advective inputs, conduction may be second in importance after solar inputs. Conduction from near stream soils and alluvial substrates may account for more of the stream temperature dynamics than is generally recognized (Hondzo and Stefan 1994). Several physical factors contribute to these fluxes of heat. First, heat exchange occurs from materials at higher temperatures to those at lower temperatures, and second, the rate of heat transfer between water and substrates is three orders of magnitude greater than the rate between water and air (Monteith and Unsworth 1980). Moreover, a large amount of stream water may be in contact with substrates, especially during subsurface and hyporheic flow. In this study, stream temperatures under forest cover were cooler than surface or subsurface soil temperatures in the daytime or at night. In forest gaps or disturbed riparian areas, direct solar radiation increases the temperature of soils and alluvial substrates that could conduct heat to the streams (Hondzo and Stefan 1994; Evans et al. 1995). Conduction from alluvial substrates might explain the observed increases in minimum stream temperatures after forest harvest.

Conduction can have different a magnitude of influence on stream temperature in bedrock versus alluvial reaches. Large variations in maximum and minimum stream temperatures presently occur along the length of the recently disturbed channel in WS 3; these temperature variations coincide with erosional and depositional areas and corresponding changes in types of substrates and flow paths of water (S.L. Johnson, unpublished data). Debris flows in 1996 resulted in less increase in stream temperatures at the downstream gauging station than the 1964 debris flows. Conduction between stream water and continuous bedrock, especially relating to minimum temperatures, would have different dynamics than conduction in alluvial substrates, possibly as a function of temperature gradients within bedrock.

Stream discharges, which decline through the summer in western Oregon, have been suggested as an influence of the timing of maximum summer stream temperatures (Brown 1969). In these forested basins, there is a temporal lag between maximum solar inputs in June and maximum stream temperatures in late summer. However, we found the timing of stream maxima to be unrelated to the seasonal pattern of discharge in unshaded streams. If the timing of summer high stream temperatures was driven by low stream flows, and given that flows declined in a similar manner in both harvested and unharvested basins, then the highest temperatures in both basins should have occurred at the time of lowest flows. Instead, stream temperatures in the clear-cut basin reached high levels by late June, while those in the shaded channel increased more slowly through the summer. Discharge is a factor in stream temperature budgets (Brown 1969), as a function of the volume and the residence time of water, but increased direct solar inputs appeared to be the dominant influence of the timing of maximum temperatures in streams without riparian vegetation.

Stream temperatures returned to preharvest levels in WS 1 approximately 15 years after clear-cutting, coinciding with canopy closure in the riparian zone. Although some studies have observed a trend of decreasing maxima with each year postharvest (Moring 1975; Swift 1982), our results fit more closely to the temperature recovery trajectory postulated by Beschta and Taylor (1988), who suggested that limited riparian vegetation regrowth during the first 5 years postharvest would not affect high maximum stream temperatures but that during the next 15 years, the recovery of riparian vegetation would lead to a linear decrease in stream temperatures. Although our sites had similar trajectories of temperature recovery and returned to preharvest levels, the species composition of the overstory riparian vegetation shifted from primarily conifer to deciduous. Because of potential variation in factors influencing riparian vegetation recovery among sites and regions, the timing of riparian vegetation establishment and stream temperature recovery

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Fig. 5. In 1967, (*a*) maximum and minimum daily stream temperatures for the clear-cut basin (WS 1) (black line) and unharvested basin (WS 2) (grey line) from June through September, (*b*) maximum and minimum daily stream temperatures for the basin with patch cuts and debris flows (WS 3) (black line) and the unharvested basin (WS 2) (grey line), (*c*) differences between daily maximum stream temperature for WS 1 and WS 2 (black line) and WS 3 and WS 2 (grey line), and (*d*) calculated daily solar radiation.

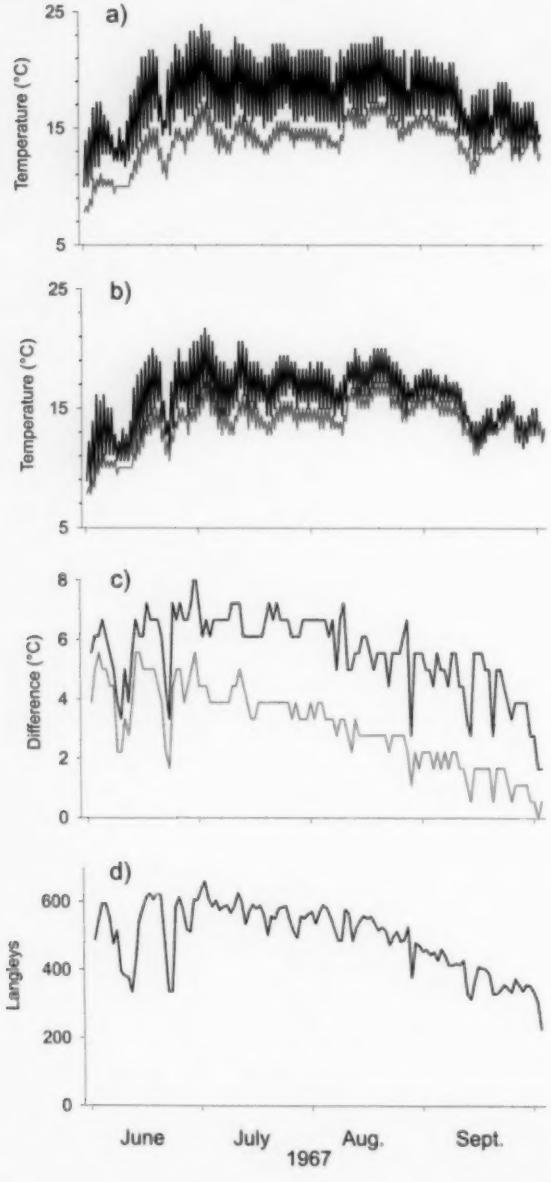
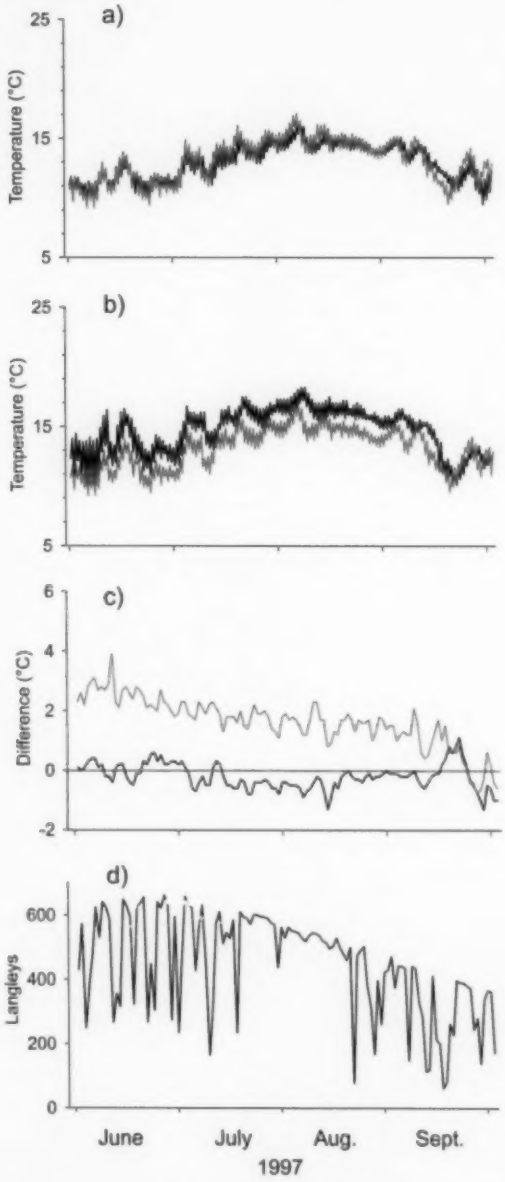


Fig. 6. In 1997, (*a*) maximum and minimum daily stream temperatures for the clear-cut basin (WS 1) (black line) and unharvested basin (WS 2) (grey line) from June through September, (*b*) maximum and minimum daily stream temperatures for the basin with patch cuts and debris flows (WS 3) (black line) and the unharvested basin (WS 2) (grey line), (*c*) differences between daily maximum stream temperature for WS 1 and WS 2 (black line) and WS 3 and WS 2 (grey line), and (*d*) measured daily solar radiation.



cannot necessarily be extrapolated to other locations without consideration of specific processes and mechanisms.

Biotic implications

Changes in the seasonal timing of increased temperatures may have subtle but important effects on stream biota. The greater increases in early summer stream temperatures documented in this study coincide with early developmental stages of many organisms, possibly leading to different types of impacts than if temperature increases primarily oc-

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Fig. 7. Cumulative degree-days, calculated beginning June 1, using mean daily stream temperature for the clear-cut basin (WS 1) (black line), unharvested basin (WS 2) (dotted line), and the basin with patch cuts and debris flows (WS 3) (grey line) in (*a*) 1967 and (*b*) 1997.

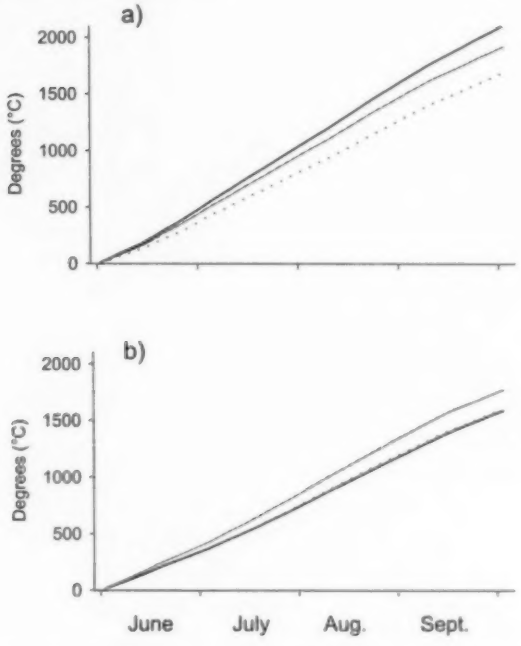
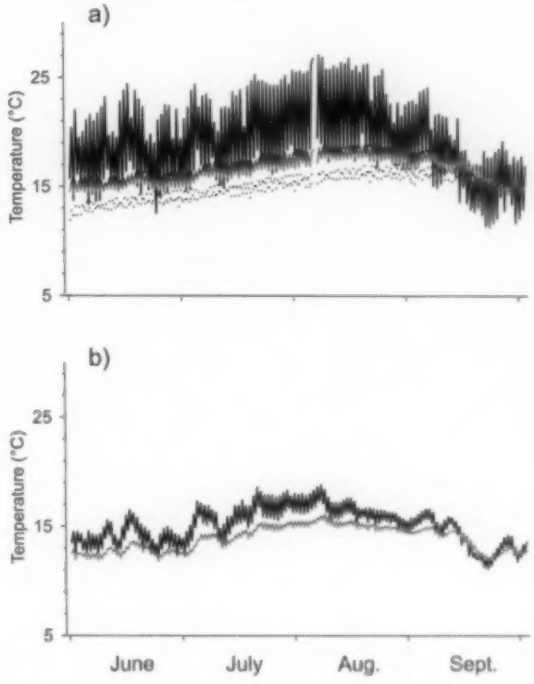


Fig. 8. Maximum and minimum daily soil temperature in 1997 (*a*) 10 (black line), 50 (grey line), and 100 cm (dotted line) below the surface in the forest gap (primary climate station), and (*b*) 10 (black line) and 30 cm (grey line) below the surface in an old-growth forest (WS 2 reference stand).



curred at times of historical maximum summer temperatures. Aquatic organisms are quite sensitive to changes in stream temperatures (e.g., Beitinger and Fitzpatrick 1979; Vannote and Sweeney 1980; Ward and Stanford 1992); increases in maximum stream temperature can be lethal, but increases of sublethal temperature result in changes in metabolism and growth rates (Medvick 1979; Thomas et al. 1986) as well as changes in food web dynamics and competitive interactions (Brett 1952; Reeves et al. 1987). Higher temperatures require more energy from biota to sustain increased rates and processes and can deplete the energy reserves of individual fish (Thomas et al. 1986). Increased temperature can also lead to greater virulence of bacterial diseases (Becker and Fugihara 1978) at a time when individuals are being subjected to thermal stress and have reduced resistance (Thomas et al. 1986). Upper thermal limits for organisms vary by species and life stage of the organism (Brett 1952; Coutant 1977), with the young generally being most sensitive to increases in the temperature of their environment.

Increased rates of accumulation of thermal degree-days, as observed in this study, have been shown to affect life history patterns and timing of emergence of biota. Following forest harvest in a coastal Oregon stream, an average subsurface stream temperature increase of 1.5°C in coho salmon (*Oncorhynchus kisutch*) spawning beds was estimated to shorten the incubation period of salmon eggs by 13 days (Ringler and Hall 1975). In a stream in British Columbia, juvenile coho salmon smolts grew more rapidly following clear-cutting and an increase in stream temperatures and migrated earlier to the ocean than before forest harvest (Holtby 1988). Earlier migration of these smolts may have led to reduced survival rates due to increased exposure to migrating predators (Holtby 1988). Aquatic macroinvertebrates are also impacted by changes in stream temperatures (Vannote and Sweeney 1980; Ward and Stanford 1992). Higher stream temperatures resulted in more rapid growth of invertebrates through their instar phases and hatching at smaller sizes (Vannote and Sweeney 1980).

The increased range of variation in stream temperature at diurnal, weekly, and seasonal time scales shown in this study could have important biological impacts (Medvick 1979; Thomas et al. 1986). Generally, in undisturbed forested streams, the range of temperature variation increases with length of time over which data are evaluated, leading to greater variation at the seasonal scale than at the diurnal scale. However, after clear-cutting and burning, the diurnal range of temperature in early summer (6–8°C) was as great as the seasonal range in an unharvested basin (8°C). Similar diurnal increases have been found in other regions (Swift 1982; Lynch et al. 1984). These rapid fluctuations in temperature could lead to stress for organisms (Thomas et al. 1986), although the specific tolerances and responses of most organisms to rapid temperature fluctuations are not well known.

In summary, not only were maximum and minimum stream temperatures higher following clear-cutting, but the temperature differences between shaded and unshaded streams were greatest early in the summer season. Our re-

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sults support the hypotheses that stream temperatures in these basins are driven by fluxes of shortwave solar radiation that can be modified by riparian shading and that conduction from the soils and alluvial substrates is of greater importance than generally recognized. Although regrowth of deciduous riparian vegetation resulted in a return to preharvest stream temperatures approximately 15 years postharvest, site-specific factors may produce shorter or longer recovery times for stream temperatures at other sites. There is a need to better understand the spatial and temporal factors influencing the direct shading of stream channels for successful riparian restoration activities to moderate high stream temperatures. Research on the potential for heat dissipation through interaction of stream water with shaded alluvial substrates is also needed. In addition, studies of the effects of wide diurnal stream temperature fluctuations on aquatic biota would be very valuable.

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Assessment of changes in lake pH in southeastern Canada arising from present levels and expected reductions in acidic deposition

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Abstract: An integrated acid rain assessment model was used to estimate pH for six clusters of lakes in southeastern Canada and scenarios of sulphate deposition that reflect the situation (*a*) before implementation of the SO_2 emission controls required by the Canada/U.S. Air Quality Agreement, (*b*) after implementation of Canadian controls, and (*c*) after implementation of Canadian and U.S. controls. Modelled lake pHs were always less than their estimated original values. To assess the ecological significance of the pH reduction, scenario "damage" was quantified as the percentage of cluster lakes having pH < 6, a threshold criterion sufficient to protect most aquatic biota. Care was taken to account for naturally acidified lakes. The integrated acid rain assessment model predicted that Canadian SO_2 controls will reduce damage in Ontario and Quebec but have little effect in Atlantic Canada. Implementation of U.S. SO_2 controls will further reduce damage throughout all regions, although it is conservatively estimated that from 5 to 24% of the lakes will still have pH < 6 depending on cluster. Extrapolating to the inventory of acid-sensitive lakes in southeastern Canada suggests that ~76 000 lakes and ~970 000 ha of lake area will remain chemically damaged unless additional reductions in SO_2 emissions are implemented beyond those required by the Air Quality Agreement.

Résumé : Nous avons eu recours à un modèle intégré d'évaluation des pluies acides pour estimer le pH de six groupes de lacs du sud-est du Canada et élaborer des scénarios de dépôt de sulfate qui reflètent la situation (*a*) avant la mise en oeuvre des limitations des émissions imposées par l'Accord canado-américain sur la qualité de l'air, (*b*) après la mise en oeuvre des limites canadiennes, et (*c*) après la mise en oeuvre des limites des deux pays. Les pH des lacs modélisés étaient toujours inférieurs aux valeurs initiales estimées. Pour évaluer la signification écologique de la réduction du pH, les « dommages » des scénarios ont été quantifiés comme le pourcentage des lacs du groupe présentant un pH < 6, critère seuil suffisant pour protéger la plus grande partie du biote aquatique. On a pris soin de tenir compte des lacs naturellement acidifiés. Le modèle a prédit que les limitations canadiennes des émissions de SO_2 vont réduire les dommages en Ontario et au Québec, mais auront peu d'effet au Canada atlantique. La mise en oeuvre des limitations des États-Unis contribuera à réduire les dommages dans toutes les régions, mais une estimation prudente montre que 5% à 24% des lacs auront encore un pH < 6 selon le groupe. Si on extrapole pour l'ensemble des lacs vulnérables à l'acidification dans le sud-est du Canada, on peut penser que ~76 000 lacs et ~970 000 ha de superficie de lacs resteront chimiquement affectés, à moins que soient mises en oeuvre des réductions supplémentaires des émissions de SO_2 par rapport aux limites fixées par l'Accord.

[Traduit par la Rédaction]

Introduction

Surface water acidification by "acid rain" gained prominence as an environmental issue in Canada during the 1970s. Beamish and Harvey (1972) and Beamish (1976) had observed losses of fish species in the La Cloche Mountain lakes of Ontario that they linked to acidification caused by atmospheric deposition of pollutants presumed to originate from the nearby smelters at Sudbury. Others soon demonstrated that lake acidification was a more widespread phenomenon (e.g., Dillon et al. 1978; Watt et al. 1979). This initiated more than a decade of intense research and monitoring to document and predict the extent and magnitude of aquatic effects in Canada (see reviews by Harvey et al. 1981; RMCC 1990). Similar concern and action also developed in the United States (Irving 1991).

The scientific consensus on aquatic effects obtained during the 1980s significantly influenced the political process that resulted in formalization of the 1991 Canada/U.S. Air Quality Agreement (AQA) (see Canada/U.S. 1992) and establishment of SO_2 and NO_x emission control targets for both countries. Under the AQA, Canada was committed to reaching a national SO_2 emission cap of 3.2×10^6 tonnes $SO_2 \cdot year^{-1}$ by 2000 and a cap for the seven eastern provinces of 2.3×10^6 tonnes $SO_2 \cdot year^{-1}$ (~40% reduction from the 1980 level) by 1994. The United States was committed to reducing SO_2 emissions by 10×10^6 tons $SO_2 \cdot year^{-1}$ from

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1980 levels by 2000 to attaining a national cap of 8.95×10^6 tons $SO_2 \cdot year^{-1}$ for electric utilities by 2010 and to maintaining a 5.6×10^6 tons $SO_2 \cdot year^{-1}$ cap for industrial sources beginning in 1995 (also ~40% reduction overall from the 1980 level). Note that the differing mass units for Canadian and U.S. emissions are as specified in the AQA (Canada/U.S. 1992).

In response to AQA commitments, both Canada and the United States have significantly reduced SO_2 emissions. Total North American emissions are now ~30% less than in 1980. Canada attained both of its AQA targets by 1993, and in 1997, SO_2 emissions were 18 and 24% below the national and eastern caps, respectively (Canada/U.S. 1998). Similarly, 1997 U.S. SO_2 emissions nationally were 24% below 1980 levels and further reductions are expected as Phase II of Title 4 of the U.S. Clean Air Act Amendments is implemented between 2000 and 2010. In contrast with the SO_2 reductions, North American NO_x emissions have increased slightly since 1980 (Environment Canada 1997).

The purpose of this paper is to assess the ecological adequacy of AQA-required SO_2 emission control programs by evaluating the changes in lake pHs expected to occur in six regions of southeastern Canada. The evaluation will use the integrated acid rain assessment model (IAM) of Lam et al. (1998) to predict lake pH as a function of SO_2 emission levels and extends work previously reported by Jeffries (1997).

Some changes in precipitation and surface water chemistry that are likely related to emission reductions have been observed already. For example, decreasing SO_4^{2-} trends have been detected throughout northeastern North America in both precipitation (Sirois 1993) and lakes (Clair et al. 1995; Stoddard et al. 1999). However, observation of corresponding increases in water pH or alkalinity have been much less uniform, indicating that these ecosystems are still adjusting to the reduced acidifying input. Concurrent declines in base cation concentrations (Jeffries et al. 1995; Likens et al. 1996; Stoddard et al. 1999), increasing NO_3^- (Couture 1995), desorption of SO_4^{2-} from soil organic matter (Alewell et al. 1999), and oxidation of reduced sulphur compounds stored in wetlands or other ecosystem compartments (Dillon et al. 1997) have all been shown to cause a lack of conformity between SO_4^{2-} and pH/alkalinity trends and to delay acidification recovery.

Water pH plays an important role in determining the presence/absence or success of aquatic species, and much research during the 1970s and 1980s focussed on identifying the pH tolerance limits for reproduction and survival of specific groups of organisms (see reviews by Baker et al. 1990; RMCC 1990). While some aquatic species (e.g., rotifer (*Keratella* spp.), dragonfly (*Leucorrhinia glacialis*), yellow perch (*Perca flavescens*)) are relatively insensitive to reduced pH and are found across a broad pH range, many others species (e.g., the amphipod *Hyallela azteca*, certain mayfly species (Ephemeroptera), certain crayfish species (*Orconectes*), lake trout (*Salvelinus namaycush*)) are negatively affected when water pH decreases. Hence, biological communities in acidified lakes tend to have a lower biodiversity than those in circumneutral lakes. In addition, Doka et al. (1997) showed that pH is a consistent and significant determinant of species richness and occurrence for several aquatic taxa in eastern Canada, even after accounting for other potentially confounding factors such as Al and (or) dissolved organic carbon (DOC) concentrations, geographic location, and lake morphometry. For this reason, we have selected pH as the assessment variable for this paper.

Materials and methods

Lake chemistry

The lake chemistry compilation of Jeffries (1997) for Ontario and eastwards was used in this analysis. Water samples included in the database were limited to those collected in 1985 and later. This "sampling date" screen was used to select major element data (pH, Ca^{2+}, Mg^{2+}, Na^+, K^+, Gran alkalinity, SO_4^{2-}, NO_3^-, Cl^-, DOC) from an earlier database (Fraser et al. 1990) for all provinces except Ontario. For Ontario, the current version of the "acid lakes database" (cf. Neary et al. 1990) was screened. More recent data from McNicol et al. (1996) for Ontario and Nova Scotia, Kelso et al. (1992) for central Ontario, Clair et al. (1995) for Nova Scotia, Newfoundland, and Quebec, and Dupont (1992*a*, 1992*b*) and Papineau (1996) for southern Quebec and unpublished data for New Brunswick (W. Pilgrim, New Brunswick Department of Environment, personal communication) were added also. The Laurentian Great Lakes are not part of the database. Neither are the meagre data available from Prince Edward Island because its terrain is insensitive to acidification. Overall, the database contains 8874 samples from 2831 lakes.

The database is not representative of the population of ~800 000 water bodies extant in southeastern Canada (Hélie et al. 1993), first because of the necessity of compiling it from multiple sources and second because regional lake surveys in Canada have generally not employed a statistically based sampling design like that used in the United States (Landers et al. 1988) or Fennoscandia (Henriksen et al. 1990). A notable exception was the "Québec lake survey" in southwestern Quebec (Dupont 1992*a*, 1992*b*), which was designed to be representative of the 10–2000 ha size-class of lakes. Even then, while fairly representative of the areal water resource, the Québec lake survey is not representative in terms of numbers, since Hélie et al. (1993) found that 80% of the lake population in southern Quebec is <5 ha in size. Across all regions, small lakes are greatly underrepresented in our database.

The spatial distribution of lakes in the database varies greatly from province to province (Fig. 1), ranging from fairly uniform and comprehensive coverage in southern Quebec to clusters of lakes in Nova Scotia, New Brunswick, and Ontario. Many of the areas in eastern Canada without data are outside the region of significant acidic deposition (e.g., northern Quebec and Ontario) or in areas of insensitive terrain (e.g., portions of Nova Scotia, New Brunswick, and southern Ontario).

Data quality was evaluated by calculating sample charge balances. Sixty-two percent of the samples in the database had enough major ion variables reported to permit this calculation. Cations and anions in 80% of this subset usually balanced within ±15% or better. Whenever possible, organic anions were included in the balance by estimation from DOC and pH (modified after Oliver et al. 1983). The water chemistry submodels contained in the IAM require a single sample with the same variables as those used to calculate a charge balance, including DOC. Many lakes had multiple samples in the database, and in such cases, a synthetic sample composed of median variable concentrations was determined for model input. This procedure served to improve the quality of the data used for modelling.

Selection of lake clusters

To accommodate the lack of spatial continuity in contemporary survey data (Fig. 1), six clusters of lakes were identified for modelling purposes: southern Nova Scotia – New Brunswick (S. NS-

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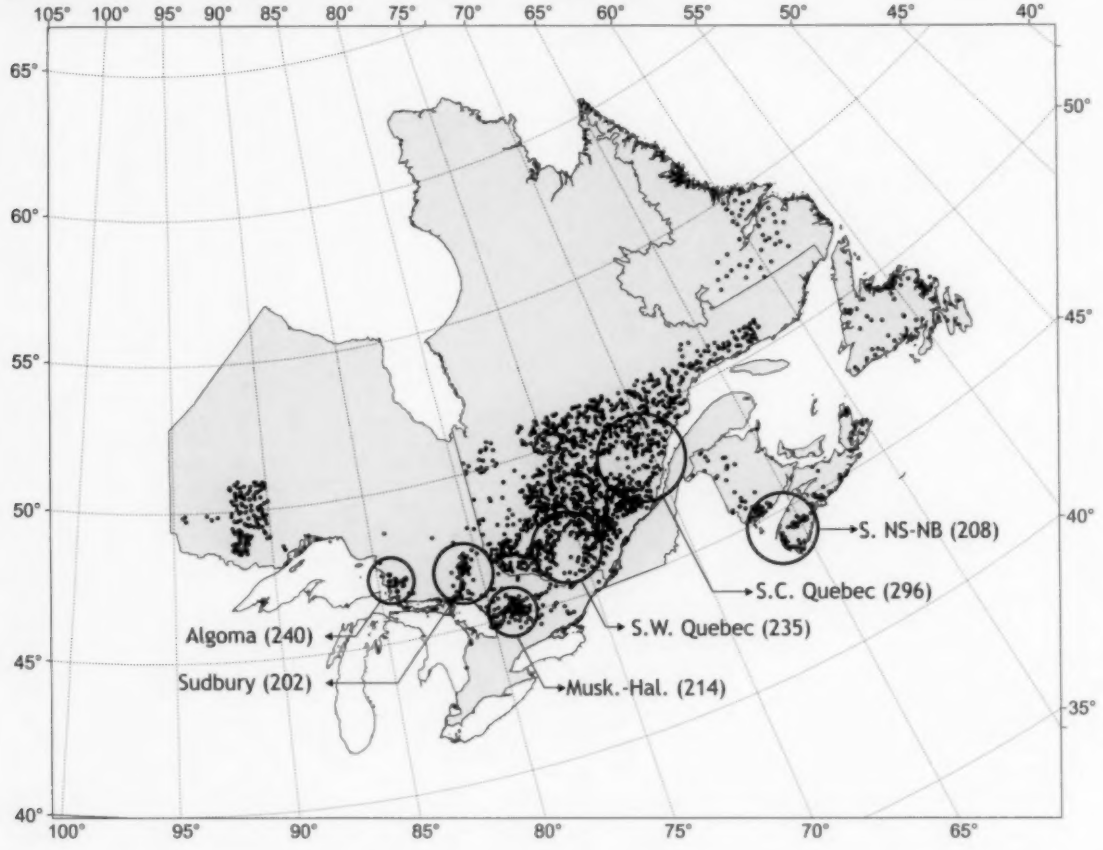
Fig. 1. Spatial distribution of lakes included in the chemistry database. Note that there are many cases where the locator dot for one lake overlaps others. Locations of the six lake clusters used to assess "damage" are shown by the open circles, and the number of sample lakes suitable for modelling in each cluster is indicated beside the name.



NB), south-central Quebec (SCQ), southwestern Quebec (SWQ), and Muskoka–Haliburton (M-H), Sudbury, and Algoma in Ontario. Cluster selection criteria included reasonable uniformity of terrain characteristics and enough lakes having complete ion chemistry (a modelling requirement) to permit meaningful statistical evaluation of the modelling results. Hence, the clusters are not uniform in size (Fig. 1) and the number of lakes contained in a given cluster ranged from 202 to 296 (Table 1). One cluster (S. NS-NB in Fig. 1) contained two geographically separated regions with 97 of its 208 lakes located in southwestern Nova Scotia and the remainder located in sensitive terrain in southern New Brunswick.

Modelling approach

Although some European models were available (e.g., Amann 1990; Hordijk 1995), the IAM used here was developed to take advantage of the data sources and types available in North America. The IAM is not a single model but rather a framework of submodels and (or) cause–effect relationships (for details, see Lam et al. 1998). For this paper, two IAM components have been used, an atmospheric source–receptor relationship linked to an expert system of water chemistry models.

The atmospheric source–receptor relationship was used to predict seasalt-corrected wet SO_4^{2-} deposition received by all the lakes in each cluster. It was obtained from runs of the continental-scale source–receptor model of Olson et al. (1983) using SO_2 emission data for 40 North American source regions and meteorological information from either 1980 or 1985. The IAM's single source–receptor relationship is an optimal combination of the annual source–receptor matrices for the two meteorological years. The source–receptor relationship estimates wet SO_4^{2-} deposition, but total (wet plus dry) SO_4^{2-} deposition is required to run the water chemistry models. Total deposition was obtained by adding an estimate of dry deposition to the wet component. As rationalized by RMCC (1990), dry constituted 15% of the total for all clusters except Sudbury where 50% was used.

The total SO_4^{2-} deposition estimates were input to the expert system of water chemistry models to predict the pH of cluster lakes (for details, see Lam et al. 1992). As configured in the IAM, the expert system uses one or more of four steady-state models to compute lake alkalinity. Lake pH is subsequently estimated from a pH–alkalinity relationship (modified after Small and Sutton 1986). The automated choice of model(s) to predict alkalinity is based on a set of rules that use measured sample alkalinity and DOC levels as selection criteria. The rules were established using both knowledge of which model is most appropriately applied to a given lake chemistry and testing to optimize prediction accuracy, hence the term "expert" system. The IAM uses steady-state water chemistry models because the required input data are modest compared with time-dependent models, and their predictions have a common frame of reference, i.e., after equilibration to a given SO_4^{2-} deposition. While time-dependent models could provide information on response time as well as eventual condition, input data require-

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Table 1. Number of lakes and estimated sea-salt-corrected, wet SO_4^{2-} deposition for the six lake clusters (see Fig. 1) and three SO_2 emission scenarios (see text).

		Wet SO_4^{2-} deposition ($kg \cdot ha^{-1} \cdot year^{-1}$)				
Cluster	No. of lakes	Scenario 1	Scenario 2	Scenario 3	Background*	Lakes with $pH_o < 6$ (%)
S. NS-NB	208	14.4	13.6	12.0	5.6	50.9
SCQ	296	21.6	18.7	16.4	4.8	2.7
SWQ	235	21.1	18.3	14.9	3.9	2.1
M-H	214	24.3	22.7	18.9	4.0	0.5
Sudbury	202	25.6	21.5	17.8	3.5	3.5
Algoma	240	19.3	17.2	14.0	3.6	0.4

Note: The estimated background component included in the deposition scenarios and the estimated percentage of lakes having original pH (pH_o) < 6 for each cluster are shown also. Scenario deposition values given here are for a specific receptor location in the middle of each cluster. Scenario deposition for individual lakes were determined by kriging and differ slightly.

*Background deposition determined from the product of an assumed wet deposition SO_4^{2-} concentration of 0.4 $mg \cdot L^{-1}$ and climatological precipitation.

ments would eliminate a large proportion of the lakes available for assessment.

Propagation of error through the IAM's submodels and determination of the overall error have been evaluated (for details, see Lam et al. 1992, 1998). Lam et al. (1992) showed that the expert system accurately simulated observed alkalinity and pH distributions for several regional data sets when contemporary SO_4^{2-} deposition was used as the driving input and that the overall relative error in the median pH (estimated for regional subsets of lakes) was 20–30%.

Neither the effect of nitrogen deposition nor decreasing base cation deposition were considered in our model runs. At present, nitrogen-based water acidification is of minor regional importance (Jeffries 1995), e.g., provincial median lake NO_3^- is only 1% (Ontario) to 7% (Quebec) of the median SO_4^{2-} concentrations (Jeffries 1997). Decreasing base cation deposition may be of potentially greater regional significance than nitrogen, since declining trends have been identified (Summers 1995; Environment Canada 1997), but with no means of projecting future levels, base cation deposition was held constant throughout the scenario simulations. If either nitrogen or reduced base cation deposition had been included in the model, the resulting lake pH estimates would be lower.

SO_4^{2-} deposition scenarios

Lake pH was estimated for three SO_2 emission scenarios. Scenario 1 (S1) approximates the situation predating implementation of controls required by the AQA by utilizing measured Canadian and U.S. emission levels for 1985 (total SO_2 emissions = 24.6×10^6 tonnes$\cdot$year^{-1}). Scenario 2 (S2) uses measured Canadian emissions for 1994 and measured U.S. emissions for 1990 (22.7×10^6 tonnes $SO_2 \cdot year^{-1}$), thereby approximating the situation where AQA-required controls were fully implemented in Canada but not in the United States. Scenario 3 (S3) corresponds to the situation expected after full implementation of all AQA-required SO_2 controls in both countries (18.1×10^6 tonnes $SO_2 \cdot year^{-1}$). The effect of Canadian SO_2 controls on Canadian lake chemistry is therefore approximately reflected in the difference between S1 and S2, and the effect of U.S. controls is the difference between S2 and S3. Maps of predicted eastern North America wet SO_4^{2-} deposition associated with roughly equivalent SO_2 emission scenarios are presented in Environment Canada (1997). Table 1 provides estimates of sea-salt-corrected, wet SO_4^{2-} deposition for each scenario at a location in the middle of each cluster.

Original lake pH and the damage threshold pH

Estimating the change in steady-state pH (ΔpH) of lakes for a given SO_4^{2-} deposition scenario requires a reference value for comparison, either their original or preacidification pH (pH_o) or some standard value. While using pH_o has the advantage that the resulting ΔpHs are absolute estimates of acidification, the ecological significance of the pH change is not readily apparent. Ecological significance is an important issue here, since we are trying to assess the effectiveness of emission controls established on the premise of improving environmental protection. Using an appropriate reference pH value to calculate ΔpH can provide the necessary ecological relevance, and several reviews (e.g., Baker et al. 1990; RMCC 1990; Doka et al. 1997) have concluded that maintenance of lake water pH $\geq$ 6 will prevent most deleterious biological effects from acidic deposition. Throughout the remainder of this paper, the estimation of aquatic ecosystem "damage" will be based on whether or not modelled lake pH for a given SO_4^{2-} deposition scenario falls below the pH 6 threshold.

The pH 6 threshold raises a methodological problem because there is a class of "brown-water" lakes that are naturally acidified by organic acids, and some, probably those with low base cation concentrations, are unlikely to ever have had pH $\geq$ 6. To deal with the problem, we have taken the simplest approach possible by identifying the subset of lakes in each cluster that had estimated $pH_o \geq 6$ (see below) and then using only this subset to assess response to the SO_4^{2-} deposition scenarios. We quantified damage by determining the number of lakes in the cluster subset that have scenario pH < 6 and then expressing it as a percentage of the overall cluster population, an approach equivalent to assuming that lakes with $pH_o < 6$ (i.e., the excluded lakes) are not damaged by any deposition scenario. This assumption is clearly not true, but using it does establish a lower boundary for the estimated damage levels and is in keeping with the other factors that also lead to conservative damage estimates (see Discussion).

The pH_o of each lake was calculated using background SO_4^{2-} deposition as an IAM input. Background SO_4^{2-} deposition (Table 1) was estimated from the product of annual precipitation and a SO_4^{2-} concentration of 0.4 $mg \cdot L^{-1}$, a value derived from an analysis of 1985–1995 precipitation chemistry from remote sampling sites in the Northwest Territories, northern Saskatchewan, and Labrador (R. Vet, Meteorological Service of Canada, personal communicatiom). The percentage of sample lakes in each cluster estimated to have $pH_o < 6$ is given in Table 1. These are the lakes excluded from the damage estimation. Five of the six clusters have small numbers of lakes (0.4–3.5% of the sample populations) with pH_o below the pH 6 threshold, and hence, the $pH_o \geq 6$ subset differs by only a small degree from the entire sample population. S. NS-NB is an exception. Slightly more than half of its lakes have estimated $pH_o < 6$ so that the $pH_o \geq 6$ subset differs significantly from the entire sample population.

Damage extrapolation

There is a need to extrapolate cluster damage estimates to the broader lake resource. To do this, we have used the resource inven-

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Table 2. Number of lakes and total surface area for three data sets associated with each of the lake clusters: (*a*) for lakes with measured area from the cluster sample, (*b*) for all lakes from TWS that contain sample lakes and are within the measured size range of the Sample Subset (as specified), and (*c*) for the entire lake resource from TWS containing sample lakes.

Cluster (no. of TWS)	Data category	No.	Area (ha)
S. NS-NB (15)	(*a*) Sample Subset (2.0–1180 ha)	85	6 000
	(*b*) TWS Subset	2 258	95 000
	(*c*) TWS Resource	5 994	196 000
SCQ (23)	(*a*) Sample Subset (2.2–1203 ha)	282	13 000
	(*b*) TWS Subset	33 187	608 000
	(*c*) TWS Resource	84 491	1 040 000
SWQ (16)	(*a*) Sample Subset (5.0–987 ha)	235	9 000
	(*b*) TWS Subset	15 122	501 000
	(*c*) TWS Resource	59 986	1 002 000
M-H (7)	(*a*) Sample Subset (2.0–2821 ha)	214	25 000
	(*b*) TWS Subset	8 125	204 000
	(*c*) TWS Resource	34 048	346 000
Sudbury (6)	(*a*) Sample Subset (0.3–1297 ha)	183	11 000
	(*b*) TWS Subset	21 652	255 000
	(*c*) TWS Resource	30 120	365 000
Algoma (4)	(*a*) Sample Subset (0.2–81.3 ha)	239	2 000
	(*b*) TWS Subset	12 987	62 000
	(*c*) TWS Resource	15 256	108 000

Note: Categories *b* and *c* were extracted from the database of Hélie et al. (1993).

tory of Hélie et al. (1993), which quantified the lake population south of 52°N and east of the Manitoba–Ontario border, the area identified as the acid rain "region of concern" by RMCC (1990). Since the chemical database is not a statistical subset of the inventory, the accuracy of extrapolating cluster damage results will always be in question. A trade-off will exist between the accuracy of such extrapolation and the spatial extent over which it is applied. To address the trade-off, we have defined a sequence of resource subsets (both lake numbers and lake surface area) for extrapolating the cluster damage estimates.

Three of the resource subsets developed for extrapolating damage estimates are summarized in Table 2. The first resource subset was simply the lakes from each cluster sample for which surface area was known and will henceforth be termed the "Sample Subset" (data category *a* in Table 2).

Other resource subsets were developed using the Hélie et al. (1993) inventory, which is organized according to tertiary watersheds (TWS). A TWS is that unique drainage basin defined by the Water Survey of Canada obtained from a third-level subdivision of the four primary basins that compose southeastern Canada. The Hélie et al. (1993) inventory covers 309 TWS, and we identified the TWS associated with each cluster through a GIS overlay of sample lake latitudes/longitudes (number of TWS indicated in Table 2).

The "TWS Resource" subset (data category *c* in Table 2) was obtained by extracting from the Hélie et al. (1993) database the overall inventory of lakes within all the TWS associated with each cluster. The TWS Resource subset contains ~25% (numbers and area) of the entire southeastern Canada inventory. The "TWS Subset" (data category *b* in Table 2), which is intermediate between the Sample Subset and the TWS Resource, was obtained by extracting those lakes from the TWS Resource that covered the lake area size range present in the Sample Subset. The TWS Subset constitutes 11% of the number of lakes and 14% of the lake area in the entire inventory.

Despite increasing uncertainty, even greater extrapolation is necessary to give a realistic impression of the overall effect of AQA-required emission controls on southeastern Canadian lakes. Straightforward scaling of the cluster damage estimates to the overall inventory is unwise, however, because it covers all levels of terrain sensitivity. Fortunately, Hélie et al. (1993) also identified the number and area of lakes in each province that are sensitive to acidic deposition by overlaying the inventory on the database of soil and bedrock characteristics used to produce the national terrain sensitivity map (Environment Canada 1988). Hence, cluster damage estimates were extrapolated to these provincial subsets of sensitive lakes: the estimate for S. NS-NB was applied to the sensitive inventory component from Nova Scotia and New Brunswick (12 714 lakes, 196 000 ha), the mean estimate from SCQ and SWQ was applied to Quebec (353 000 lakes, 5 140 000 ha), and the mean estimate from M-H, Sudbury, and Algoma was applied to Ontario (195 000 lakes, 1 710 000 ha). No damage extrapolation was made to the Newfoundland subset.

Results

Change in cluster pHs versus deposition scenario

Examples of the pH distributions calculated by the IAM for background SO_4^{2-} deposition and the three scenarios are illustrated in Fig. 2. Percentile statistics for ΔpH (calculated as $pH_{Scenario} - pH_o$, which yields negative values for a pH decline) are presented in Table 3. In general, pH values are lowest in S. NS-NB and highest in the Ontario clusters. S. NS-NB is the only cluster in which a large fraction (more than half) of its lakes had estimated $pH_o < 6$ (Table 1), and indeed, more than 25% of its lakes had $pH_o < 5$ (Table 3). This regional pattern for lake acidity in southeastern Canada has been noted previously (e.g., RMCC 1990; Jeffries 1997) and is primarily caused by regional differences in bedrock and surficial geology and to a lesser degree by differences in hydrological characteristics and (or) the prevalence of natural acidification by organic acids.

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Fig. 2. Examples of cluster pH distributions for (*a*) SCQ and (*b*) Algoma estimated by the IAM for background SO_4^{2-} deposition (pH_o) and the three deposition scenarios (as labelled).

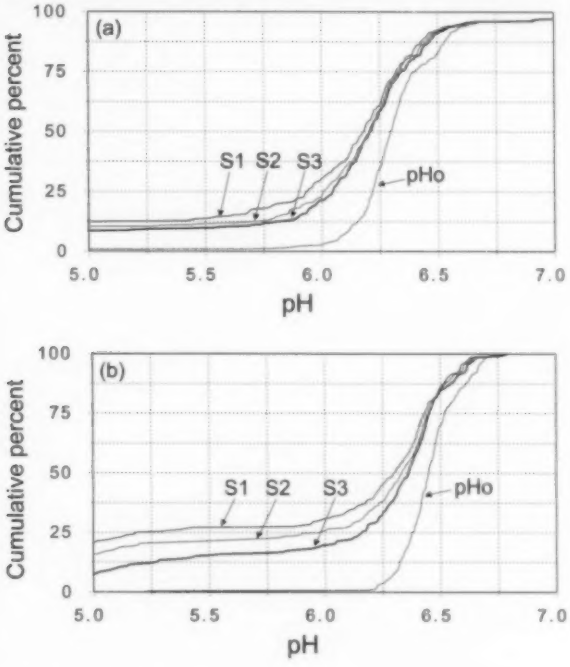
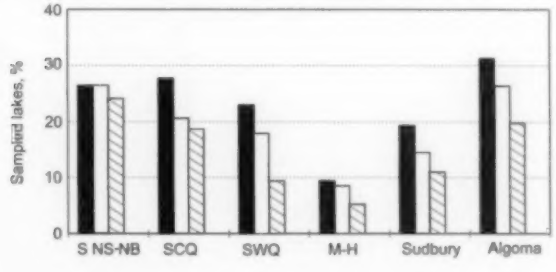
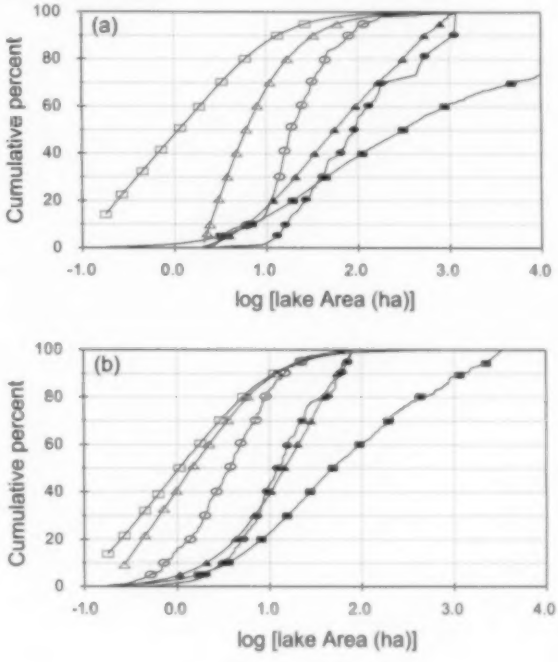


Fig. 3. Estimated percentage of lakes in the six clusters damaged under SO_4^{2-} deposition scenario S1 (solid bars), S2 (open bars), and S3 (hatched bars). Percent damage was quantified for the subsets of lakes with $pH_o \geq 6$ relative to the overall cluster sample. This is equivalent to assuming that lakes with $pH_o < 6$ are not damaged and yields conservatively low values.



The pH distribution curves in Fig. 2 for the four levels of SO_4^{2-} deposition (background plus the three scenarios) illustrate the fact that elevated SO_4^{2-} deposition most strongly affects the more acid-sensitive lakes in each cluster. The separation between the curves is greater at lower pH. Median ΔpH (Table 3) ranged from only –0.05 (Sudbury, S3) to –0.22 (S. NS-NB, S1) whereas the 75th percentile ΔpH ranged from –0.13 (SWQ and M-H, S3) to –1.26 (S. NS-NB, S1). Differences between scenario distributions are relatively minor for lakes with estimated pHs greater than ~6.3. The scenario and pH_o distribution curves tend to coalesce at pH > 6.5 in the upper 20–25% of the pH distributions for all

Fig. 4. Examples of the distribution of lake numbers and lake area for (*a*) SCQ and (*b*) Algoma for the three data categories described in Table 2: Sample Subset (numbers, open circles; area, solid circles), TWS Subset (numbers, open triangles; area, solid triangles), and TWS Resource (numbers, open squares; area, solid squares).



clusters except S. NS-NB (~5%). In general, the IAM predicts that declining SO_4^{2-} deposition results in less negative ΔpHs from S1 to S2 to S3, but even after all AQA emission controls are implemented (S3), a substantial ΔpH continues to exist.

Cluster damage versus deposition scenario

As noted above, the ecological significance of the increase in lake pH predicted to result from reduced SO_4^{2-} deposition has been quantified using a pH 6 threshold applied only to the cluster subset having estimated $pH_o \geq 6$. For all clusters except S. NS-NB, the subset is a close approximation of the entire sample population. The percentage of damaged lakes (i.e., having estimated steady-state pH < 6) for each of the three scenarios is presented in Fig. 3. As a general observation, the percentage of damaged lakes decreases from S1 (pre-AQA SO_2 emission levels) to S3 (full implementation of AQA SO_2 controls) for all clusters.

Damage levels for S. NS-NB cover a very narrow range (26% for S1 to 24% for S3), showing that the AQA-required emission reductions will have only a minor effect on this region of Atlantic Canada. The damage magnitude is similar to the S1 levels calculated for several other clusters despite the fact that S. NS-NB has the lowest scenario deposition values (Table 1). This reflects the extreme acid sensitivity (low base cation and alkalinity concentrations) of waters in the region (Jeffries 1997). S. NS-NB is the one cluster where

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Table 3. Percentile statistics for the original pH (pH_o) and change in pH (ΔpH) associated with each of the three SO_4^{2-} deposition scenarios.

			ΔpH ($pH_{scenario} - pH_o$)		
Cluster	Percentile	pH_o	Scenario 1	Scenario 2	Scenario 3
S. NS-NB	25th	4.68	–0.10	–0.09	–0.08
	50th	5.98	–0.22	–0.21	–0.16
	75th	6.15	–1.26	–1.23	–1.15
SCQ	25th	6.22	–0.08	–0.07	–0.06
	50th	6.30	–0.13	–0.11	–0.09
	75th	6.40	–0.29	–0.21	–0.17
SWQ	25th	6.18	–0.07	–0.06	–0.05
	50th	6.25	–0.14	–0.12	–0.09
	75th	6.52	–0.23	–0.18	–0.13
M-H	25th	6.47	–0.06	–0.05	–0.04
	50th	6.51	–0.11	–0.10	–0.08
	75th	6.55	–0.20	–0.18	–0.13
Sudbury	25th	6.37	–0.01	–0.01	–0.01
	50th	6.46	–0.08	–0.07	–0.05
	75th	6.52	–0.31	–0.20	–0.14
Algoma	25th	6.38	–0.08	–0.07	–0.06
	50th	6.45	–0.17	–0.13	–0.10
	75th	6.52	–1.06	–0.39	–0.23

Note: All values were estimated by the IAM as described in the text.

the subset of lakes having $pH_o > 6$ differ greatly from the overall sample. In this case, the decision to express the percent damage relative to the overall sample yields values that we interpret as a lower boundary. If the percentage is expressed relative to the number of lakes in the subset, the values range from 54% (S1) to 49% (S3). For the remaining clusters, expressing damage relative to the subsets yields almost the same values as those shown in Fig. 3 because the subsets differ so little from the overall sample populations.

Estimated damage for the Quebec clusters ranged from 28% for S1 in SCQ to 9% for S3 in SWQ (Fig. 3). Across all three scenarios, damage levels for SWQ are lower than those for SCQ. Lower SO_4^{2-} deposition resulting from implementation of Canadian SO_2 controls reduced the estimated lake damage in SCQ and SWQ by 7 and 5%, respectively (difference between S1 and S2). Implementation of AQA-required SO_2 controls in the United States (S3) further reduced damage in both clusters, although the effect was much more pronounced in SWQ.

In Ontario, estimated damage varied among both the three clusters and the three SO_4^{2-} deposition scenarios (Fig. 3): Algoma consistently showed the highest levels (31% for S1 to 20% for S3), Sudbury was intermediate (19% for S1 to 11% for S3), and M-H was lowest (9.4% for S1 to 5.1% for S3). The higher damage levels estimated for Algoma may reflect the higher proportion of small lakes in its sample population (see Discussion). Canadian SO_2 controls reduced damage in all three clusters, although the relative impact on M-H was much smaller than on Sudbury or Algoma. Complete implementation of U.S. emission controls further reduces damage in all three Ontario clusters, and for the M-H cluster in particular, reducing U.S. SO_2 emissions was relatively more influential than reducing Canadian emissions.

Damage extrapolation

Using SCQ and Algoma as examples once again, the cumulative percent distributions of both lake numbers (open symbols) and lake area (solid symbols) as a function of area are shown in Fig. 4 for the three data sets defined in Table 2 (i.e., the Sample Subset, the TWS Subset, and the TWS Resource). Note that the horizontal scales are expressed as log[lake area] to improve the readability of the plots. Figure 4 illustrates the fact that a large fraction (80–90%) of lakes in the TWS Resource are 10 ha (i.e., log[1.0] on the horizontal scale) or smaller, but these lakes constitute a small fraction (<5–20%) of the areal lake resource (also see Hélie et al. 1993).

Damage estimates for the situation when all AQA-required SO_2 emission controls are fully implemented in Canada and the United States (i.e., S3 values in Fig. 3) were applied to the extrapolation data sets and are presented in Table 4. The most conservative and probably reliable extrapolation involves using the TWS Subsets, i.e., limiting the extrapolation to only those TWS Resource lakes that are within the same size range as the Sample Subset. This approach estimated that a total of ~13 000 lakes of ~230 000 ha will have a $pH < 6$ even after all AQA-required SO_2 emission reductions are implemented.

Extrapolation beyond the size range of the Sample Subset but confining it to the TWS that have sample lakes (i.e., the TWS Resource data set) is a less conservative approach. It estimates that a total of ~31 000 lakes of ~410 000 ha will remain damaged after S3 conditions are attained.

Scaling the S3 damage estimates to the provincial, sensitive subsets of the Hélie et al. (1993) inventory is the least conservative extrapolation, but it does provide an order-of-magnitude impression of the overall effectiveness of AQA-required emission reductions in controlling acid rain aquatic effects. This extrapolation suggests that ~3050 lakes (~47 000 ha) in Nova Scotia and New Brunswick, ~49 000 lakes (~720 000 ha) in Quebec, and ~23 000 lakes (~200 000 ha) in Ontario for a total of ~76 000 lakes

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Table 4. Extrapolated number of lakes and total surface area predicted to remain damaged (steady-state pH < 6) after full implementation of all AQA-required SO_2 emission controls (S3).

Cluster	S3 damage (%)	Data category	No.	Area (ha)
S. NS-NB	24.0	(*b*) TWS Subset	542	23 000
		(*c*) TWS Resource	1 439	47 000
SCQ	18.6	(*b*) TWS Subset	6 173	113 000
		(*c*) TWS Resource	15 715	193 000
SWQ	9.4	(*b*) TWS Subset	1 421	47 000
		(*c*) TWS Resource	5 639	94 000
M-H	5.1	(*b*) TWS Subset	414	10 000
		(*c*) TWS Resource	1 736	18 000
Sudbury	10.9	(*b*) TWS Subset	2 360	28 000
		(*c*) TWS Resource	3 283	40 000
Algoma	19.6	(*b*) TWS Subset	2 545	12 000
		(*c*) TWS Resource	2 990	21 000
		Total (*b*) TWS Subset	13 455	233 000
		Total (*c*) TWS Resource	30 802	413 000

Note: The extrapolation has been applied to the TWS data sets defined in Table 2.

(~970 000 ha) will remain damaged (i.e., steady-state pH < 6) under the S3 level of SO_4^{2-} deposition.

Discussion

This paper has had to confront the incompatibility of providing supportable, policy-relevant predictions of the broad-scale effect of reducing acidifying emissions based on lake chemistry data that are not representative of the overall resource. It was deemed essential that any conclusions indicating a need for further emission reductions be based on conservative rather than speculative science. We therefore used the data characteristics and certain methodological choices to ensure that our damage estimates are conservative, i.e., if anything, underestimates.

The sample bias towards larger lakes should yield conservative damage estimates. As illustrated by the separation of the Sample Subset distribution curves for lake numbers (open circles in Fig. 4) from the TWS Resource and TWS Subset curves (open squares and triangles, respectively), our cluster data sets clearly contain a higher proportion of larger lakes. Note that the Sample Subsets more closely approximate the resource distribution of lake area than of lake numbers, i.e., in Fig. 4, there is a lesser separation between the Sample Subset and TWS Subset distributions for lake area (solid circles and triangles, respectively) than the equivalent distributions for lake numbers (open circles and triangles, respectively). Hence, extrapolating damage estimates based on lake area may provide more reliable values within the size range of the Sample Subset than extrapolating damage based on numbers.

The size distribution of the Algoma Sample Subset (Fig. 4*b*) is the least biased of all the clusters due to the inclusion of several small lakes from the database of McNicol et al. (1996). The fact that Algoma's damage estimates were unexpectedly high relative to the other, more biased Ontario clusters supports the general belief that larger lakes are likely to be less acid sensitive.

The SCQ Sample Subset (Fig. 4*a*) is composed of data that primarily originated from two sources, i.e., mostly from Dupont (1992*a*), which were collected to statistically represent the 10–2000 ha size fraction, plus a smaller (~10%) component that focussed on small lakes (Papineau 1996). The resulting structure of the SCQ Sample Subset gives the bimodal shape of the distribution curve that runs roughly parallel to the TWS Subset curves but are shifted to the right. If the data from Papineau (1996) are excluded from the Sample Subset, then it and the TWS Subset curves will approximately coincide, as would be expected to result from the statistically based sampling design of Dupont (1992*a*).

Several of our methodological choices result in conservative damage estimates. They include limiting the damage analysis to only the lake subsets having $pH_0 \geq 6$ and then expressing the percent damage relative to the whole cluster set, using the pH 6 threshold, including only SO_4^{2-} deposition as the model driver (i.e., not including nitrogen-based acidification), maintaining base cation deposition constant, and not including sensitive Newfoundland/Labrador lakes (as identified by Hélie et al. 1993) in the extrapolation analysis. The reason for including use of the pH 6 threshold in the list is because Jeffries (1997) showed that choosing less ecologically supportable thresholds such as pH 5.5 or pH 5.0 did not decrease the damage estimates and in some cases gave the counterintuitive result of increasing the damage. This occurred because some of the very sensitive lakes with $pH_0 < 6$ must be included in the $pH_0 \geq 5.5$ and $pH_0 \geq 5.0$ subsets where they are no longer automatically counted as unaffected in a damage analysis.

The pH responses predicted to occur in the six lake clusters show that SO_2 emission controls implemented in Canada or expected in the United States result in reduced damage levels. S. NS-NB is the least influenced by the emission controls (i.e., minimal between-scenario differences), which is not surprising, since existing SO_2 control strategies have focussed on reducing the magnitude and spatial extent of the high deposition "bullseye" that covers southern Ontario, Quebec, and the midwestern United States. An emission control strategy focussing on the Atlantic provinces and the New England states will be needed to significantly reduce lake damage in S. NS-NB.

For the Quebec and Ontario clusters, our analysis predicts that both Canadian and U.S. emission reductions will be

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influential in reducing damage. The pattern of between-scenario changes in lake damage differs between clusters in a way that seems to reflect the relative geographical proximity of the clusters to U.S. source regions. For example, reduction in percent damage for the most distant cluster (SCQ) is more associated with Canadian emission controls (difference between S1 and S2 in Fig. 3) and less associated with U.S. emission controls (difference between S2 and S3). In contrast, damage reduction for the most southerly clusters (SWQ and M-H) is more associated with U.S. controls. Note that since data characteristics, modelling, and damage estimation procedures are constant from one SO_4^{2-} deposition scenario to another, differences between the scenario damage levels are subject to the least error possible.

Across all clusters, estimated damage levels will range from 5% (M-H) to 24% (S. NS-NB) after all the emission controls required by the AQA are implemented. Just what damage level is acceptable is a political decision. The recent "Canada-Wide Strategy on Acid Rain" (based on AETG 1997) has established a policy goal of reducing SO_4^{2-} deposition to the critical load in Canada. Determination of critical loads for aquatic ecosystems in Canada has employed a 5% damage limit (RMCC 1990; Jeffries et al. 1999), and so it is clear that further reduction in SO_2 emissions in both Canada and the United States will be needed to achieve the goal. Dupont (1993) reported damage estimates using the pH < 6 criterion for five regions of southern Quebec for both the late 1980s (cf. S1) and a reduced deposition scenario similar to S3. He estimated damage ranging from 29% (Saguenay) to 66% (North Shore) in the late 1980s and from 8% (Saguenay) to 58% (North Shore) under reduced SO_4^{2-} deposition. Our damage estimates for the Quebec clusters are at the low end of Dupont's (1993) range, both because of the conservative approach that we have adopted and because we have not included a cluster equivalent to his North Shore region where natural organic acids are the primary acidifying agent.

Extrapolation of the S3 damage estimates to the regional lake populations translates the predicted influence of the AQA into more concrete terms. Restricting the extrapolation to those TWS that contain sample lakes capable of having pH ≥ 6 suggests that at least 13 000 lakes or 233 000 ha of lake area (based on the TWS Subset) to perhaps as many as 31 000 lakes or 413 000 ha (based on the TWS Resource) will have a steady-state pH < 6 after the benefits of all AQA-required SO_2 controls are fully realized. Extrapolating even further to the provincial subsets of sensitive lakes quantified by Helie et al. (1993) increases the estimate of post-S3 damage to 76 000 lakes (8.5% of the entire inventory) or 970 000 ha (8%). The uncertainty in these results is impossible to quantify precisely, but for the reasons discussed above, they most likely underestimate the real situation. The important point is that any of the damage extrapolations (underestimated or not) represent a large and continuing resource loss.

Our damage estimates are in reasonable agreement with those from other assessments. Minns et al. (1992) estimated that ~78 000 lakes will have pH < 6.0 under a deposition scenario similar to S3, although they included lakes that had pH_0 < 6.0. For that part of Quebec south of 51°N and a target population encompassing the 10–2000 ha size range, Dupont (1993) estimated that ~23 000 lakes capable of having pH > 6.0 would still not meet this criterion after implementation of controls. Our damage extrapolation (~49 000 lakes) using the subset of sensitive Quebec lakes is of the same order of magnitude as Dupont's (1993) and probably even a reasonable match given that over 80% of the Quebec lake population is <10 ha in area (see the TWS Resource distribution for SCQ in Fig. 4*a*) and the Hélie et al. (1993) inventory covers a larger area (i.e., to 52°N).

The magnitude of the damage estimates leaves little doubt that the AQA offers insufficient protection from acidic deposition for lake ecosystems in southeastern Canada. AETG (1997) suggested that a further reduction in North American SO_2 emissions in the 50–75% range may be needed to obtain sufficient protection.

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Century-long effects of forest harvest on the physical structure and autotrophic community of a small temperate lake

N.M. Scully, P.R. Leavitt, and S.R. Carpenter

Abstract: The effects of forest clearcut and regrowth on a small (8.1 ha) stained lake were studied using a 200-year record of fossil carotenoids and chlorophylls. Comparison of high-resolution cores recovered from exposed, sheltered, and reference lake basins showed that annual laminations of sediments ceased concomitant with logging (ca. 1870–1890), indicating a fundamental change in the lake mixing regime. Biological responses to forest harvest included elimination of deepwater populations of anaerobic photosynthetic bacteria and reduced abundance of metalimnetic chrysophytes. Photosynthetic bacteria remained absent for over 100 years, while sediment laminae and chrysophytes have only returned since around 1970. In contrast, populations of epilimnetic phytoplankton (cyanobacteria, chlorophytes, cryptophytes) were unaffected by the clearcut. Analysis of sediment profiles did not reveal evidence of eutrophication or of increased flux of organic matter following watershed disturbance. Instead, fossil records were most consistent with increased wind stress, leading to deeper water column mixing in fall and reduction in deepwater anoxia, the main factor promoting sediment laminations and populations of photosynthetic bacteria. Such century-long disturbance may be common in small, stratified boreal lakes that lack physical shelter due to landforms.

Résumé : Nous avons étudié les effets de la coupe à blanc et de la régénération sur un petit lac (8,1 ha) aux eaux sombres en examinant sur 200 ans la présence de caroténoïdes et de chlorophylles fossiles. La comparaison de carottes à haute résolution obtenues dans des bassins de lacs exposés, abrités et témoins a révélé que les laminations annuelles des sédiments ont cessé en même temps que commençait l'exploitation forestière (v. 1870–1890), ce qui indique un changement fondamental dans le régime de mélange des lacs. Les réactions biologiques à l'exploitation forestière étaient notamment l'élimination des populations profondes de bactéries photosynthétiques anaérobies et une baisse de l'abondance des chrysophycophytes métalimnétiques. Les bactéries photosynthétiques sont restées absentes pendant plus d'un siècle, tandis que les lames des sédiments et les chrysophycophytes ont refait leur apparition à peu près depuis 1970. Par contre, les populations de phytoplancton épilimnétique (cyanobactéries, chlorophytes, cryptophytes) n'ont pas été affectées par la coupe à blanc. L'analyse des profils des sédiments n'a montré aucun signe d'eutrophisation ou d'augmentation du flux de matières organiques après la perturbation du bassin hydrographique. Les données fournies par les fossiles correspondaient surtout à une augmentation de la tension du vent, qui provoquait un mélange plus profond de la colonne d'eau à l'automne et une réduction de l'anoxie en eau profonde, principal facteur favorisant la lamination des sédiments et la multiplication des bactéries photosynthétiques. De telles perturbations s'étendant sur un siècle peuvent être courantes dans les petits lacs stratifiés de la zone boréale qui, à cause du relief, sont dépourvus d'abris physiques.

[Traduit par la Rédaction]

Introduction

Logging activity in western North American forests has doubled every 20 years since 1920 (Hartman and Scrivener 1990), whereas similar levels of intense harvest have been recorded in many forested areas of North America during the past 150 years (e.g., Lott et al. 1994). Comparative surveys of lakes in recently cut, burned, and reference ecosystems suggest that logging can lead to brief (2–10 years) increases in the inputs of nutrients (Rask et al. 1993, 1998), dissolved organic matter (DOM) (Carignan et al. 2000), contaminants (Hg) (Garcia and Carignan 1999), or mineral matter (Lott et al. 1994), often due to elevated terrestrial export in streams (Borman et al. 1974; Hartman and Scrivener 1990). As well, forest removal may lead to increased surface windspeed (Schindler et al. 1990), deepened lake mixing (France 1997; cf. Steedman and Kushneriuk 2000), and elimination of anoxic habitats in small, stratified boreal lakes (Rask et al. 1993). However, to date, no study has quantified the relative impact on lake biota of chemical and physical changes arising from forest harvest.

Recent research suggests that algal and invertebrate responses to modern forestry practises are often slight (Rask et al. 1993; Patoine et al. 2000) and not easily distinguished from background environmental variation (Paterson et al.

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1998). Increased nutrient flux stimulates algal production on a volumetric basis (Rask et al. 1993); however, concomitant increases in the dissolved organic C content or turbidity of lakes (Carignan et al. 2000) may reduce light penetration, areal production, and the scope for planktonic response (cf., Christensen et al. 1996; Carpenter et al. 1998). Although forest harvest by ancestral Europeans altered planktonic communities for several decades (e.g., Davis and Norton 1978; Lott et al. 1994), impacts of clear-cutting are not easily distinguished from those of subsequent agricultural activities. Effects of clearcut on mixing regimes in lakes may be more long-lived (~100 years; France 1997), but insufficient data exist to evaluate this hypothesis.

We used a 200-year record of fossil pigments to investigate how forest harvest has altered the mixing regime and microbial food web composition of a small temperate lake during the past 100 years. Comparison of fossil profiles in exposed, sheltered, and reference lake basins suggested that epilimnetic phytoplankton communities varied little in response to forest removal but that clear-cutting increased wind access to the lake, accentuated water column mixing in fall, and eliminated deep layers of photosynthetic bacteria and chrysophytes. These changes have remained evident even after 75 years of forest regrowth.

Materials and methods

Site description

Long Lake is an 8.1-ha, twin-basin seepage lake located on the University of Notre Dame Environmental Research Center in Michigan (46°32′N, 89°32′W) (Fig. 1). The west and east basins are 17.7 and 14.4 m deep, respectively, and are connected by a shallow channel that drains into bogs through an intermittent outflow (Christensen et al. 1996; Cole and Pace 1998). Prior to whole-lake experiments in 1991, epilimnetic waters (~0–3 m) were stained (g_{440} = 0.5–1.2·m^{-1}, Kd_{PAR} = 1.0–1.5·m^{-1}, dissolved organic C = 7–9 mg·L^{-1}), slightly acidic (pH 5.5–6.5), and moderately productive (~6 μg chlorophyll (Chl)·L^{-1}, alkalinity = 0.71 mg·L^{-1} as $CaCO_3$, total P = 14 μg·L^{-1}; Christensen et al. 1996). Midsummer hypolimnetic waters are cold (6°C), dark, and anoxic (oxygen < 1 mg·L^{-1}), except in the channel where thermal stratification is poorly defined.

Prior to 1991, Long Lake supported native populations of largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieui*), and yellow perch (*Perca flavescens*). *Chaoborus flavicans* and *Chaoborus punctipennis* were the main pelagic invertebrate predators, while *Polyphemus* sp. was common in the channel. Large *Daphnia pulex* dominated the biomass of herbivorous zooplankton (~50%), although *Holopedium*, small calanoid copepods, and rotifers were also numerous (Carpenter et al. 1996). Summer phytoplankton communities were composed mostly of chrysophytes in June and July (*Chrysospharella*, *Dinobryon*, *Synura*, *Kepherion*) and chlorophytes later in the summer (*Sphaerocystis*, *Teracystis*, *Arthrodesmus*, *Eurastrum*) (UNDA 1988; Carpenter et al. 1996). Changes in planktonic communities since 1991 (after core collection) are described in Cottingham and Carpenter (1998) and Carpenter et al. (1998). In particular, recent observations show that metalimnetic blooms of chrysophytes were present in the west basin of Long Lake during 1990–1991 (Christensen et al. 1996). *Sphagnum* and macrophytes are occasionally present in the lake margins, similar to other lakes in the region. Sedges, leatherleaf, and lilies are also common near the edge of the channel.

Long Lake lies within 2 km of Peter, Paul, and Tuesday lakes, similar sites with well-documented limnological (Carpenter et al. 1996, 1998) and paleolimnological histories (Leavitt et al. 1989, 1993; Carpenter and Leavitt 1991) but contrasting exposure to forestry practises. For example, Tuesday Lake is surrounded by an extensive bog mat, has relatively little forest within in its catchment, and can be used as an unharvested reference ecosystem. In contrast, the drainage basin of Peter and Paul lakes experienced a harvest history similar to that of Long Lake (Leavitt et al. 1989), but the lakes are well sheltered from prevailing winds by steep moraine ridges in comparison with the more exposed basins of Long Lake (fig. 1 in Cole and Pace 1998). Consequently, comparisons of published fossil records (Leavitt et al. 1989, 1993; Carpenter and Leavitt 1991) with new analyses from Long Lake can provide insights into the causes of past limnological and environmental changes.

Disturbance history

The watershed of Long Lake was undisturbed prior to 1852 (UNDA 1988) (Table 1). Survey maps from that era show that the first-growth forest consisted of hemlock, birch, sugar maple, balsam, and cedar. Logging company records show that regional forests were clearcut during 1870–1890 (UNDA 1988), although the specific years of cutting around Long Lake are not known. Lumber companies operated a logging camp and railroad line in the Long Lake watershed during 1917–1924. Casual reference to the region near Long Lake states that the land was "barron or covered with popple and young hard maple" in 1932 (UNDA 1988). No further logging occurred until 1950–1960 when selective removal of aspen was allowed. Christensen et al. (1996) documented that the present shoreline vegetation of tamarack, black spruce, and alder extends into an upland forest or either balsam fir (east basin) or red and sugar maples (west basin).

Wildfires are common after clearcuts (Vogl 1970), and the area around Long Lake burned in 1910 and again in 1913 (M. Gillen, cited in UNDA 1988). The last fire in the region occurred ca. 1924 (Leavitt et al. 1989). Further minor disturbance occurred when a road was cut along the abandoned railway line in the western watershed during 1942. Aerial photographs show that the road was extended through the east basin between 1947 and 1960 (UNDA 1988). Unlike Peter, Paul, and Tuesday lakes, Long Lake was not subject to chemical and food web manipulations during 1950–1990 (Leavitt et al. 1993) and remained undisturbed until isolation of the east and west basins with plastic barriers (1991) and experimental fertilization (1993–1997; Carpenter et al. 1998).

Sediment analyses

Sediments were collected by freeze-corer from the deepest portion of each basin of Long Lake in August 1990. Frozen cores were prepared for fine-interval sampling by removing the outermost 5 mm of sediment and freeze-drying the cleaned core for 24 h at 0.1 Pa (Leavitt et al. 1989). Individual annual laminae (varves) in sediments older than 1885 were isolated manually at −8°C within 12 h of freeze-drying sediments. More recent sediments and those from the east basin were sampled in 2.5- to 3-mm increments. Samples were relyophilized for 2 h and stored under a nitrogen atmosphere in the dark at −20°C for 24 h before further analysis (Leavitt et al. 1989).

Sedimentary pigments were extracted, filtered, and dried under nitrogen gas following the procedures of Leavitt et al. (1989). Carotenoid, chlorophyll, and derivative concentrations were quantified using a Waters HPLC system following the reversed-phase procedure of Leavitt et al. (1989). An internal reference standard (3.2 mg·L injection solvent^{-1}) of Sudan II (Sigma Chemical Corp., St. Louis) was injected into each sample. This dye runs at a central, unique position on the chromatogram, has carotenoid-like ab-

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Fig. 1. Morphometric map of Long Lake, Michigan, U.S.A. Cores were obtained from >14 m depth.

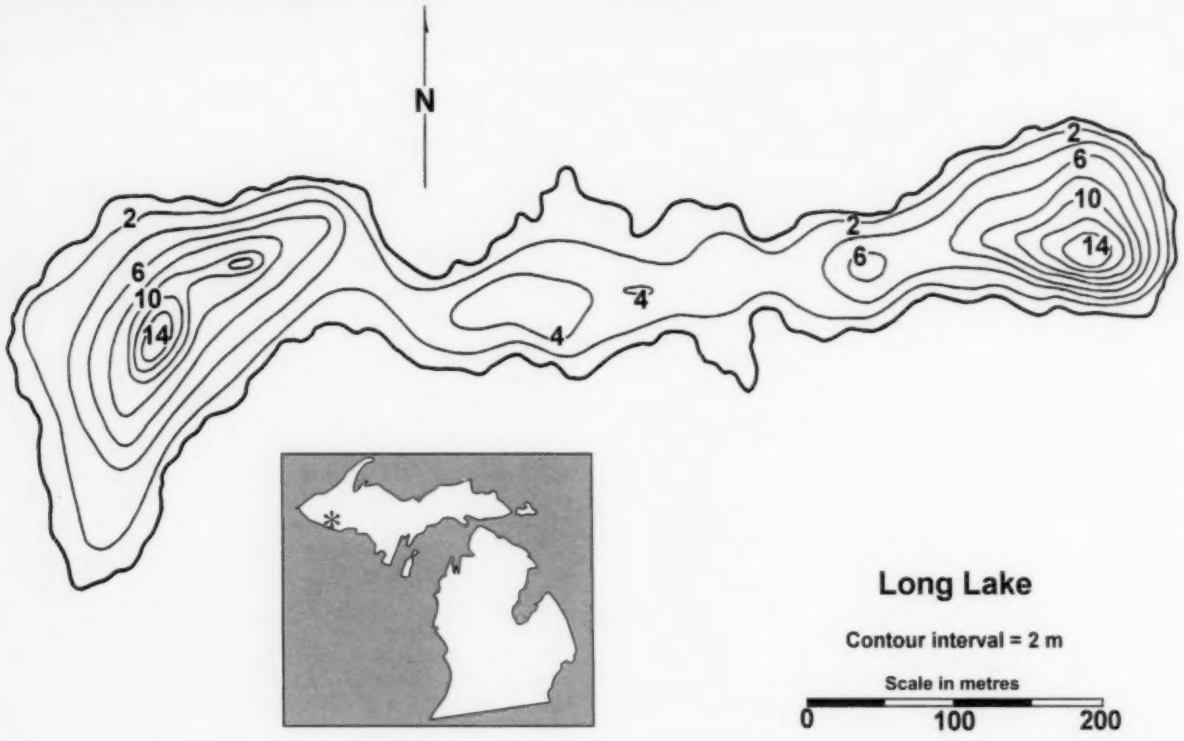

Table 1. Long Lake disturbance history, 1850–1997.

Year	Event
1852	Initial vegetation maps completed
1870–1890	Region clearcut
1910	Regional fire
1913	Regional fire
1917–1924	Lumber camp and railway in catchment
1924	Regional fire
1942	Road built in western catchment
1947–1960	Road extended into eastern catchment
1950–1960	Selective aspen harvest
1991	East and west basins isolated using vinyl curtain
1993–1997	Experimental fertilization

Note: See text for references and details. Sediment cores were collected during August 1990.

sorption characteristics (λ_{max} = 485, 442.5 nm in acetone), and is used to correct for dilution and injection errors.

Pigments isolated from sediments were compared with those from unialgal cultures. Spectral characteristics, chromatographic mobility, and functional group assays were used to identify pigments from all sources (Leavitt et al. 1989). Acid and methyl derivatives of chlorophyllous pigments were created either by aqueous alcohol extraction (chlorophyllides) or by acidification following the procedures of Leavitt et al. (1989). Not all fossil pigments were positively identified. We restrict our analysis to carotenoids characteristic of cryptophytes (alloxanthin, α-carotene in part), diatoms and chrysophytes (fucoxanthin), chlorophytes and cyanobacteria (lutein-zeaxanthin), all cyanobacteria (echinenone), and filamentous or colonial cyanobacteria (myxoxanthophyll) as well as the major *a*-, *b*-, and *c*-phorbins. In the case of Long Lake, we infer that fossil fucoxanthin mainly represents changes in chrysophyte abundance rather than diatom abundance (cf. Poister et al. 1999) both because diatom-specific carotenoids (e.g., diatoxanthin) were absent from most samples and because sediments contained mainly siliceous remains of chrysophytes (fig. 3 in Duff et al. 1995). Isorenieratene from green sulfur photosynthetic bacteria was also isolated and was indistinguishable from the authentic standard using our identification procedures (Leavitt et al. 1989). Lutein from green algae and zeaxanthin from cyanobacteria coelute on our HPLC system; consequently, pheophytin *b* was used to identify chlorophytes alone.

Pigment concentration was expressed as nanomoles of pigment per gram of organic matter. Organic matter content of varves was estimated by weight-loss-on-ignition at 500°C. This expression of fossil concentrations is directly correlated with algal standing stock and can provide reliable historical interpretations (Leavitt and Findlay 1994). Detailed discussions of pigment biogeochemistry, difficulties in fossil reconstructions, and guidelines for ecological interpretations of sedimentary records have been presented elsewhere (Cuddington and Leavitt 1999 and references therein). In addition, principal components analysis (PCA) of all fossil pigments from west basin laminated sediments was used to identify similarities in patterns of pigment deposition and to aid in stratigraphic interpretations relating to herbivore–algae interactions.

Sediment age in both basins was estimated from ^{210}Pb decay profiles using the constant initial concentration model outlined by Oldfield and Applby (1984). Use of the constant rate of supply model was precluded because accurate sampling of individual varves prevented quantitative estimation of mass accumulation rates (Leavitt and Findlay 1994). The assumption of constant sedi-

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ment accumulation rate was tested in varved sediments by plotting varve-estimated date (arbitrarily beginning 1900) versus depth. Ages of eighteenth and early nineteenth century sediments were approximated by extrapolation from ^{210}Pb age versus depth profiles.

Laminated sediments from the west basin were examined for evidence of annual cycles in microfossil deposition using a modified tape-peel technique (Davidson 1988). Algal microfossils were recovered by pressing adhesive tape to the surface of a frozen core that had been cleaned, planed, and lyophilized for 30 min. Less than 0.5 mm of sediment adhered to the tape. Tape was trimmed and fixed to an aluminum stub and coated with gold for 2 min with a Denton Desk-2 cold sputter coater. Sediments were examined under scanning electron microscopy using an Hitachi-S-2500 at 20 kV and siliceous microfossils (mainly chrysophyte cysts) identified following Duff et al. (1995).

Results

Sediment characteristics

Cores recovered from both basins of Long Lake showed evidence of rhythmic laminations. Deepwater sediments in the west basin were laminated in the upper 6–7 cm, alternating light tan layers with black sediments. Couplet thickness varied from 1.4 cm at the surface to ~3 mm at 6 cm depth, similar to annual laminations in local lakes (Leavitt et al. 1989, 1993). Laminae were rare between 7 and 26 cm depth, continuously present between 26 and 48 cm, and indistinct in the remaining 4 cm. Sediments in the east basin had live chironomids in the upper 1 cm and were unlaminated, except between 21.5 and 23.5 cm depth.

Sediment fine structure suggested that laminae in the west basin represent annual accumulations. Sediment couplets were composed of alternating bands of chrysophyte cysts and organic detritus (see fig. 3 in Duff et al. 1995) and probably represent summer and fall–winter accumulations, respectively. Similar periodicity of pigments, algae, and animal microfossils was observed in annually laminated sediments from nearby Tuesday Lake (Leavitt et al. 1993).

Analysis of the ^{210}Pb profile in the west basin suggested that varves ceased near 1885. Laminations were only present in east basin sediments between approximately 1870 and 1885. Radioisotope activity declined logarithmically with burial depth in both the east ($r^2 = 0.997$, $P < 0.0001$) and west basins ($r^2 = 0.978$, $P < 0.0001$) (Fig. 2A). The absence of substantial inflection points in either curve suggested that sediment accumulation rates have been constant through time and that the constant initial concentration model is appropriate. This hypothesis was supported by the observation that varve thickness was constant with burial depth over a 129-year varve sequence in the west basin ($r^2 = 0.997$, $P < 0.0001$) (Fig 2C). Similarly, the organic content of Long Lake sediments was relatively constant through time (Fig. 2B), as expected when allochthonous and autochthonous inputs remain constant (Rowan et al. 1992).

West basin fossil record

Total algal standing crop was inferred to have been greater during the nineteenth century than during the twentieth century in the west basin of Long Lake, when estimated using either stable fossil β-carotene (Fig. 3A) or labile Chl *a* (Fig. 3E). Concentrations of both pigments were particularly high between 1840 and 1885 but declined sharply during 1885–1900 concomitant with forest harvest and loss of sediment laminations. Both fossils showed high concentrations in surface sediments, although the greatest abundance of β-carotene occurred between 1805 and 1815 when chrysophytes bloomed. In contrast, concentrations of pigments from cryptophytes (alloxanthin, Fig. 3C), chlorophytes (lutein–zeaxanthin, *b*-phorbins, Fig. 3D), and cyanobacteria (echinenone, Fig. 3H; myxoxanthophyll not shown) were variable and showed little pattern through time in the west basin core. Green algae and cyanobacteria were apparently most common between 1850 and 1900, whereas cryptophyte

Fig. 2. Evidence for constant sediment accumulation rate in Long Lake through time from (A) linear decay rates of ^{210}Pb (1 pCi = 37 mBq) in the east (broken line) and west (solid line) basins, (B) constant weight-loss-on-ignition profiles in the east (broken line) and west (solid line) basin sediments, and (C) constant laminae thickness through time in the west basin. The year of first unambiguous varve was assigned the arbitrary year of 1900.

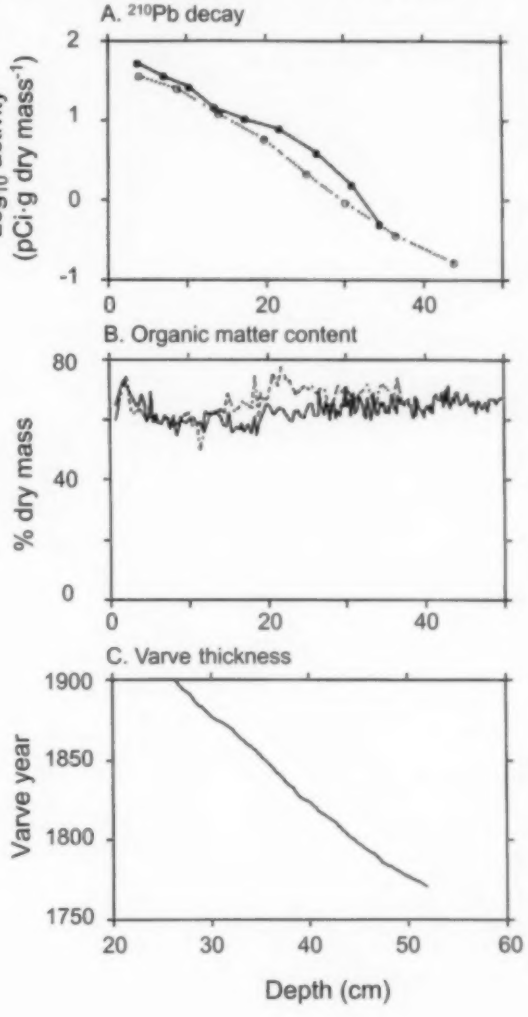

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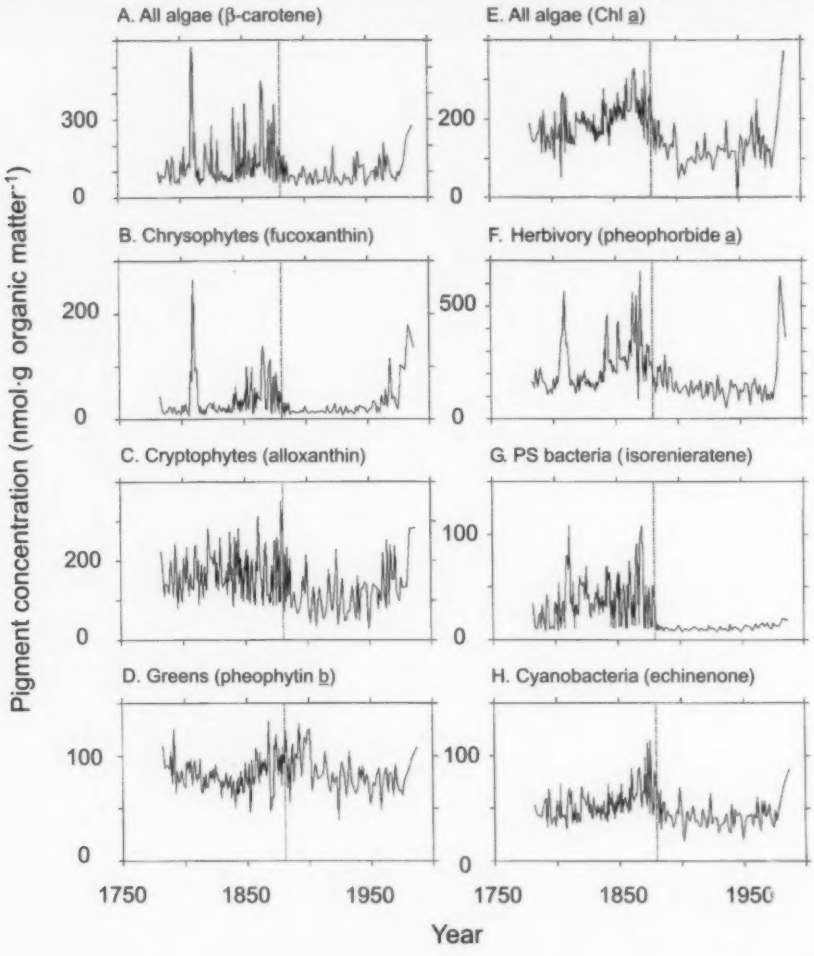
Fig. 3. Concentrations of selected fossil carotenoids, chlorophylls, and derivatives in the west basin of Long Lake. Laminations cease at a depth equivalent to 1885 and resume after ca. 1965. The vertical broken line is the midpoint of the regional forest harvest period (1880).



fossils lacked a distinctive peak but were generally reduced after 1900.

Pigments from deepwater photosynthetic bacteria declined 10-fold concomitant with forest harvest. In particular, isorenieratene from green sulfur photosynthetic bacteria was reduced to trace levels (5–10 nmol·g organic matter^{-1}) coincident with the loss of laminations from the sediments (Fig. 3G).

Fossil pigments suggested that grazing by zooplankton also influenced the vertical zonation of primary producers. Fucoxanthin from diatoms and chrysophytes showed striking peaks during 1805–1815, 1845–1885, and in recent sediments (Fig. 3B). These periods were also marked by generally high concentrations of pheophorbide *a*, a derivative of Chl *a* produced during herbivory (Carpenter and Bergquist 1985). Specifically, Pearson correlations between pheophorbide *a* and fucoxanthin (r^2 = 0.42, $P < 0.0001$) were much greater than those with pheophorbide *a* and other division-specific carotenoids (r^2 range = 0.00–0.24). Diatoxanthin from diatoms (not shown) was rare in all three periods, and its absence demonstrates that fucoxanthin was derived primarily from planktonic chrysophytes rather than from diatoms.

Multivariate analysis also suggested that chrysophyte abundance varied as a function of herbivore grazing. The first PC axis accounted for 46% of the total variance and was responsible for separating *a*-phorbins from *b*-phorbins (Fig. 4). The second PC axis contributed a further 18% of the variance and separated chrysophyte pigments (fucoxanthin, Chl *c*) from those of other algae. Pheophorbide *a* and pheophytin *a* were also clustered with pigments from siliceous algae. Finally, green algae (*b*-phorbins) were separated from cryptophytes (alloxanthin) and cyanobacteria (myxoxanthophyll, lutein–zeaxanthin in part) along the third PCA axis (11% of the total variance). This association of grazing indicator pheophorbide *a* with fucoxanthin, coupled with a virtual absence of diatoxanthin from diatoms and high numbers of chrysophyte cysts in

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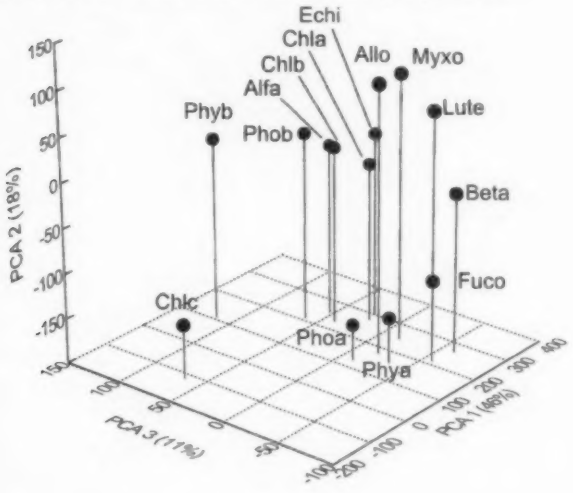
Fig. 4. PC ordination of pigments from varved sediments in the west basin of Long Lake. The first three PCA axes explain 46, 18, and 11% of the data variance, respectively. Allo, alloxanthin; Echi, echinenone; Fuco, fucoxanthin; Lute, lutein–zeaxanthin; Myxo, myxoxanthophyll; Chla, Chl *a*; Chlb, Chl *b*; Chlc, Chl *c*; Alfa, α-carotene; Beta, β-carotene; Phya, pheophytin *a*; Phyb, pheophytin *b*; Phoa, pheophorbide *a*; Phob, pheophorbide *b*.



varves (Duff et al. 1995), implied that grazing by zooplankton promoted the abundance of chrysophyte algae (cf. Leavitt et al. 1989).

East basin fossil record

Fossil indicators of total algal biomass were relatively constant with time in sediments from the east basin of Long Lake (Figs. 5A and 5B). β-Carotene concentrations were similar to those in west basin sediments but did not record maxima during the nineteenth century or in recent sediments. Chl *a* concentrations were elevated between 1850 and 1900 but did not show as great reductions after 1900 as in the west basin. Concentrations of Chl *a* were greatest during 1870–1885 when sediments were laminated.

Photosynthetic bacteria were rare in the east basin through most of the nineteenth and twentieth centuries. Isorenieratene from the Chlorobiaceae was near detection limits in the eastern core, except during 1870–1885 when sediments were laminated and during 1840–1855 when sediments were apparently homogeneous (Fig. 5G). Peak concentrations were less than half of those recorded in the western basin and almost 10-fold less than in nearby Peter and Paul lakes (Leavitt et al. 1989).

Fossil pigments from chrysophytes (Fig. 5B) were most abundant during 1850–1885 and in recent sediments, similar to patterns recorded in the west basin. Once again, concentrations of the grazing indicator pheophorbide *a* paralleled those of fucoxanthin (Figs. 5F and 5G). However, sediments from the east basin did not record a chrysophyte bloom during 1805–1815. While this may reflect differences in phytoplankton composition between basins, our east basin core may have been too short to collect these older sediments. Extrapolation of ^{210}Pb dates to sediments near 1800 was not sufficiently reliable to distinguish between these possibilities.

Pigments from cryptophytes (Fig. 5C), chlorophytes (Fig. 5D), and cyanobacteria (Fig. 5H) showed no distinctive patterns in the east basin core. Mean concentrations of alloxanthin and echinenone were the same as those from the west basin, while lutein and *b*-phorbins from green algae were 25% lower.

Sheltered and reference lakes

Detailed analyses of paleoecological records from nearby Peter, Paul, and Tuesday lakes have been published elsewhere (Leavitt et al. 1989, 1993; Carpenter and Leavitt 1991). Briefly, sediments of our undisturbed reference ecosystem, Tuesday Lake, exhibited continuous annual laminations from at least 1889 to the present (Carpenter and Leavitt 1991), while total algal abundance (as β-carotene, Chl *a*, pheophytin *a*) varied little until disturbance arising from road construction (1951), liming (1961), and food web manipulation (1961, 1985; Leavitt et al. 1993). In general, deepwater blooms of chrysophtes and sulfur bacteria were absent due to high water colour (g_{440} = 1.7·m^{-1}) and rapid attenuation of light. In contrast, sediments of sheltered Peter and Paul lakes were distinctly laminated only from 1940 onwards, and metalimnetic chrysophytes and hypolimnetic photosynthetic bacteria were common features of planktonic communities (Leavitt et al. 1989, 1993). Prior to 1940, sediment laminae were indistinct or absent, although sediment cores were too short to have encompassed the entire post-logging period. As in Tuesday Lake, total algal abundance in Peter and Paul lakes varied little in the absence of experimental manipulations (Leavitt et al. 1989).

Discussion

Comparison of fossil records among lakes suggested that forest harvest altered the fundamental physical structure of Long Lake. Annual laminations in the west basin ceased ca. 1885, concomitant with clearcut forestry practises in northern Michigan (UNDA 1988), whereas varves were continuous in undisturbed Tuesday Lake sediments. Laminations in Long Lake are composed of regular layers of chrysophyte cysts interbedded with amorphous organic matter (see fig. 3 in Duff et al. 1995) and correspond to the annual succession of summer phytoplankton and fall–spring inputs of allochthonous matter (Leavitt et al. 1993; Cottingham and Carpenter 1998). Preservation of such fine structure requires stratified, anoxic deepwaters (Anderson and Dean 1988), conditions that prevent colonization by burrowing invertebrates. Simultaneous losses of varves and obligately anaerobic photosynthetic bacteria from the west basin (see below) demonstrate that circulation of oxygen-rich waters increased following clearcut, a pattern seen in similar Finnish (Rask et al. 1993) and Canadian lakes (France 1997; but see Steedman and Kushneriuk 2000).

Analysis of the modern thermal structure of Long Lake suggested that forest harvest was unlikely to have increased lake mixing during summer sufficiently to have caused the observed changes in lake structure. Prior to experimental manipulations in 1992, the thermocline of Long Lake was at

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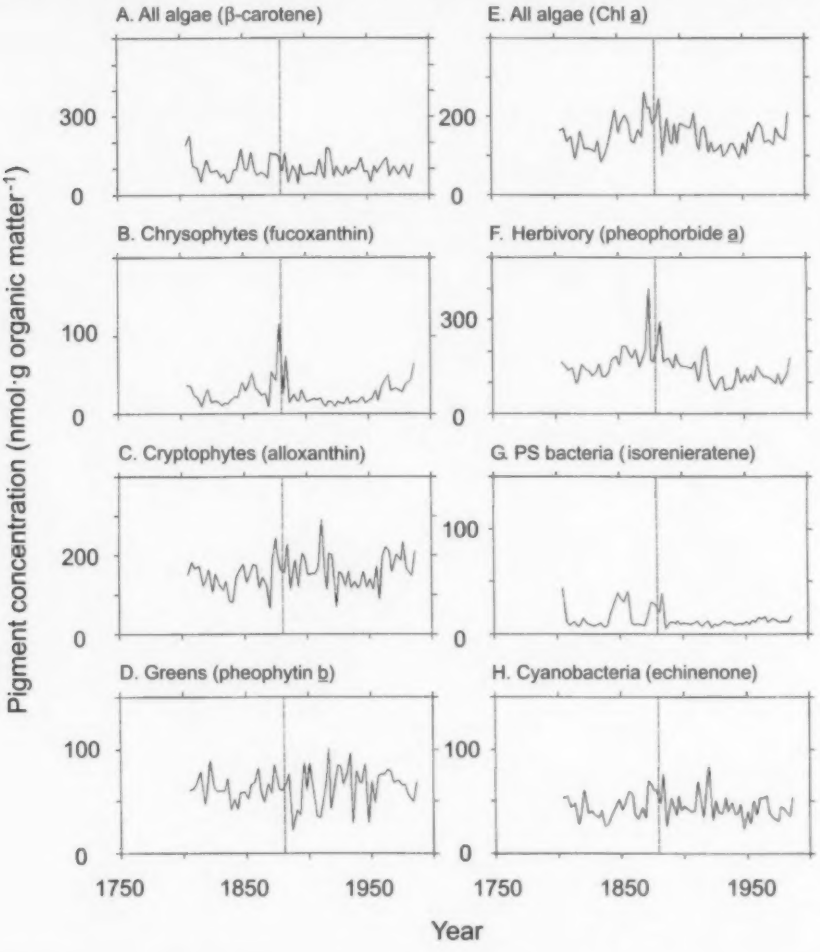
Fig. 5. Concentrations of selected fossil carotenoids, chlorophylls, and derivatives in the east basin of Long Lake. Laminations are only present between ca. 1870 and 1885. The vertical broken line is the midpoint of the regional forest harvest period (1880).



2.5 m depth during the midsummer heat content maximum (Christensen et al. 1996). As detailed by Gorham and Boyce (1989), thermocline depth at maximum heat content (Z_t) is determined by a combination of wind stress associated with summer storms (τ), maximum lake depth (Z_{max}), the density gradient between the epilimnion and hypolimnion ($\Delta\rho$), and lake length (L = area$^{0.5}$) and can be approximated for small lakes as

$$(1) \qquad Z_t = 2.0(\tau/g\Delta\rho)^{0.5}L^{0.5}$$

where g is the gravitational constant. Given the observed Z_t, and with the conservative assumption that the entire lake area contributed to lake length, we solved this equation for wind stress (τ = 0.183 N·m^{-2}) and wind speed (10.8 m·s^{-1}) associated with midsummer storms.

To evaluate the potential impact of clearcut on summer wind stress, we calculated the increase in wind stress required either to deepen the thermocline (and oxygen penetration) beyond the maximum depth of light penetration (0.1% surface irradiance, Z_p = 5.0 m) or to completely destratify Long Lake in midsummer (Z_t:Z_{max} > 0.6; Gorham and Boyce 1989). Results of this conservative analysis suggested that a τ of 0.733 N·m^{-2} (21.8 m·s^{-1}) would be required to deepen oxygen penetration beyond that of light, thereby eliminating bacterial habitat, whereas a τ of 3.05 N·m^{-2} (44.2 m·s^{-1}) would destratify modern Long Lake and eliminate varves and bacteria, as observed. Because category II hurricane winds (>42 m·s^{-1}) are unlikely in Michigan, we hypothesize that the main effects of forest harvest were felt during spring and fall, when strong seasonal winds and weak thermal stratification can combine to eliminate meromixis in small, stained lakes after a clearcut (e.g., Rask et al. 1993). Consistent with this hypothesis, sediments of the east basin, which are more exposed to storm winds from the west, were rarely laminated despite little difference in morphometry and relative depth between the east (8.4%) and west basins (8.5%). Similarly, sediments of clearcut, but sheltered, Peter and Paul lakes were only strongly laminated after 1940 despite similar relative depths (10.9 and 9.3%, respectively), suggesting that moraines reduce the effect of clearcut on lake mixing by reducing wind stress. Together, these pat-

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terns also suggest that historical changes in stratification of Long Lake did not result from regional climatic change during the twentieth century.

Watershed logging during the late nineteenth century disrupted the primary producer communities of Long Lake for over 100 years. The virtual elimination of the Chlorobiaceae concomitant with clearcut demonstrates that forest harvest eliminated the most common bacterial habitats. Green sulfur bacteria are obligate anaerobes that require light and H_2S for photosynthesis (Pfennig 1978), and their fossils indicate stable stratification of the water column and conditions where light penetrates into anoxic waters (Brown et al. 1984; Hodgson et al. 1998). Therefore, loss of photosynthetic bacteria suggests either reduced light penetration or deeper mixing, and introduction of oxygen, within the west basin of Long Lake after 1885. We argue that bacterial populations were reduced because of increased oxygen penetration (Rask et al. 1993) rather than reduced light penetration due to elevated DOM (Carignan et al. 2000), fertilization (Rask et al. 1998), or increased inorganic turbidity (Smol and Dickman 1981) because stronger light attenuation will lead to increased thermal stability and intensified deepwater anoxia during summer (Carpenter et al. 1998). These conditions should not eliminate sediment varves (Anderson and Dean 1988). Instead, oxygen is both directly toxic to the Chlorobiaceae and eliminates their electron donor for photosynthesis (H_2S; Pfennig 1978). Such Chlorobiaceae are common in local Peter and Paul lakes (Leavitt et al. 1989) and in other strongly stratified lakes (Brown et al. 1984; Hurley and Watras 1991; Hodgson et al. 1998), but only when light penetrates to anoxic waters. The continuing absence from Long Lake of such sensitive indicators strongly suggests that the impacts of logging have lasted over 100 years (France 1997).

Forest harvest reduced deepwater chrysophyte abundance in Long Lake during much of the twentieth century. Analyses of morphological (Duff et al. 1995) and biochemical fossils showed that chrysophyte blooms were common in both basins during 1850–1900, particularly during episodes of intense herbivory by zooplankton. Undisturbed, these algae grow both in the epilimnion and in dense layers just below the metalimnion in Long Lake (Christensen et al. 1996; Cottingham and Carpenter 1998) under conditions where nutrient supply saturates uptake but where light limits algal growth (St. Amand and Carpenter 1993). Although elevated nutrient or DOM inputs following clearcut (Rask et al. 1998; Carignan et al. 2000) could also eliminate metalimnetic chrysophytes from Long Lake (Christensen et al. 1996; Cottingham and Carpenter 1998; Carpenter et al. 1998), we infer that physical structure was also an important determinant of metalimnetic algal abundance because increases in the chrysophyte pigment fucoxanthin correspond closely to the reestablishment of sediment laminae ca. 1970.

Overall, clearcut practises did not greatly alter total algal production measured as either β-carotene or Chl *a*. Pigment concentrations in east basin sediments were constant through time and were similar to those in the west basin. This pattern demonstrates, therefore, that the apparent reduction of Chl *a* in western sediments after forest harvest likely resulted from reduced pigment preservation and loss of deep blooms. Pigments in metalimnetic algae are less degraded by light and oxygen and are better incorporated into lacustrine sediments, particularly for labile compounds such as Chl *a* (Leavitt et al. 1989; Leavitt and Carpenter 1990*a*). In Long Lake, the relatively constant concentrations of pigments from cryptophytes, chlorophytes, and cyanobacteria in both basins also suggest that epilimnetic phytoplankton were generally unaffected by logging. Overall, this pattern is consistent with modern (Rask et al. 1998) and fossil (Paterson et al. 1998) observations of minimal phytoplankton response to clearcut. Although increased lake circulation and oxygen transportation should also reduce overall pigment preservation in the west basin (Hurley and Armstrong 1991; Cuddington and Leavitt 1999), we infer that these changes did not substantially bias reconstructions of total algal abundance based on β-carotene because experiments in these lakes demonstrate that this compound is particularly stable in the presence of oxygen (Leavitt and Carpenter 1990*b*).

Forest harvest and subsequent fires did not greatly increase the flux of allochthonous inorganic matter to Long Lake (cf. Lott et al. 1994). Organic matter profiles in both basins showed only minor declines early in the twentieth century, consistent with relatively constant inorganic matter inputs (Rowan et al. 1992). Similarly, sediment profiles of ^{210}Pb lacked sharp discontinuities indicative of increased erosion and allochthonous inorganic influx. This result contrasts other paleoecological studies in which watershed disturbance is marked by increased water column turbidity and high mineral matter deposition (Smol and Dickman 1981; Lott et al. 1994). Input of eroded materials to Long Lake may have been reduced because of the low elevation gradient in the lake catchment (e.g., fig. 1 in Cole and Pace 1998).

Modern surveys of harvested, burnt, and reference catchments demonstrate that logging can increase water and DOM inputs to impacted lakes (Rask et al. 1998; Carignan et al. 2000). However, several lines of evidence suggest that Long Lake was not greatly influenced by these factors following clearcut. First, whole-lake experiments (Christensen et al. 1996) and comparisons with stained Tuesday Lake (Carpenter and Leavitt 1991) demonstrate that increased DOM content does not eliminate sediment varves, such as occurred in Long Lake. Similarly, reduced DOM levels are known to strongly stimulate deepwater blooms in these and other regional lakes (Leavitt et al. 1989, 1993; Hurley and Watras 1991), in constrast with observed patterns. Second, unlike in Paul and Peter lakes, there is no submerged cut or drowned timber within Long Lake, and analysis of aerial photographs (1947 to the present) shows little variation in lake level due to climatic change (Leavitt et al. 1989, 1993). This result is consistent with modern observations that Long Lake forms complex, reversible groundwater connections with other larger lakes and that it exhibits only minor (<1 m) changes in lake level (Cole and Pace 1998). Finally, elevated inputs of water, nutrients, and DOM rarely last >10 years after logging (reviewed in Keenan and Kimmins 1993); therefore, biogeochemical changes alone are unlikely to have controlled the autotrophic food web and physical structure of Long Lake for the entire twentieth century. Instead, the timeframe of Long Lake recovery is similar to that of forest regrowth, as originally proposed by France (1997).

Our analyses suggest that some biota in Long Lake may

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have benefitted indirectly from forest harvest. In general, extensive catchment clearance is known to reduce long-term fish production (Hartman and Scrivener 1990; Bérubé and Lévesque 1998) and increase their contaminant load (Rask et al. 1998; Garcia and Carignan 1999). Similarly, France (1997) suggested that cold stenotherms, such as lake trout (*Salvelinus namaycush*), might be harmed by loss of deepwater habitat. In contrast, our analysis suggested that some fish may benefit from improved lake mixing and deepwater oxygen levels by reducing the incidence of winterkill, a common feature in these lakes (e.g., Carpenter et al. 1996, 1998). Additionally, improved oxygen transport to sediments may increase the available habitat for benthic invertebrates and improve the resource base for fish. Consistent with this hypothesis, chironomids were present in surface sediments of the east basin at the time of core collection but were absent from the anoxic west basin.

Current conditions in Long Lake suggest that complete recovery from clearcut is imminent. In 1990, deep sediments of the west basin were laminated in the upper 6–7 cm, equivalent to 15–20 years of accumulation assuming that observed couplets were varves. Although oxygen still penetrates deeply during fall (Cole and Pace 1998), hypolimnetic waters are anoxic throughout the stratified period (Christensen et al. 1996) and under ice cover (J.N. Houser and S.R. Carpenter, unpublished data). In addition, metalimnetic blooms of chrysophytes and other taxa are once again common in the west basin (Christensen et al. 1996; Cottingham and Carpenter 1998). Assuming that forest regrowth was delayed about 25 years by fires during 1910 and 1913 (UNDA 1988), we estimate that even this partial lake recovery has taken over 75 years.

In summary, paleoecological analyses showed that extensive forest harvest can alter both the physical structure and autotrophic food web composition of small temperate lakes for nearly 100 years. The main effect of clearcut appears to be one of deeper lake mixing during fall or spring, resulting in increased oxygen penetration to profundal waters. We expect this effect to be particularly significant for the small, stained, stratified lakes common in the boreal forest (Rask et al. 1993) but that its importance will decrease with increased lake size (France 1997) or in lakes protected from wind by local topography. Such long-term recovery contrasts studies that suggest that nutrient and particulate flux return to normal within a decade (Keenan and Kimmins 1993). Instead, our results show that complete lake recovery is linked to forest regrowth and may take over a century.

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Phosphorus dynamics in shallow subsurface waters in an uncut and cut subcatchment of a lake on the Boreal Plain

J.E. Evans, E.E. Prepas, K.J. Devito, and B.G. Kotak

Abstract: Phosphorus dynamics in shallow subsurface waters (<2.5 m depth) were studied in harvested and unharvested subcatchments of a Boreal Plain lake. The organic soil layer was underlain by discontinuous layers of sand and clay glacial till. Total dissolved P (TDP) concentrations (6–798 $\mu g \cdot L^{-1}$) of discrete water samples from mineral layers (0.9–2.5 m deep) generally decreased with depth, were negatively related to Ca ($r_s < -0.7$), and were lower in clay. When the groundwater table rose and saturated the organic layer, TDP concentrations increased in the composite (organic mineral layer) but not in the discrete (mineral layer) water samples, indicating that elevated TDP concentrations originate from the near-surface organic layer. TDP concentrations in composite samples were negatively correlated with water table depth ($r_s = -0.6$) and were positively correlated with transmissivity ($r_s = 0.7$) and dissolved organic C concentration ($r_s > 0.6$). In the riparian buffer zone of the harvested subcatchment, TDP concentrations of composite samples decreased during high runoff, but these values remained higher than concentrations in the unharvested subcatchment. However, surface topography and variable depth to confining clay layers resulted in higher groundwater tables in the harvested subcatchment, especially in the cut area. Mean daily TDP export coefficients were similar between the unharvested (14 $\mu g \cdot m^{-2}$) and harvested (12 $\mu g \cdot m^{-2}$) subcatchments.

Résumé : La dynamique du phosphore dans les eaux subsuperficielles peu profondes (<2,5 m de profondeur) a été étudiée dans des sous-bassins exploités ou non d'un lac de la plaine boréale. La couche organique de sol reposait sur des couches discontinues de sable et de till glaciaire argileux. Les concentrations de phosphore total dissous (PTD) (6–798 $\mu g \cdot L^{-1}$) dans des échantillons discrets d'eau des couches minérales (0,9 à 2,5 m de profondeur) baissaient généralement avec la profondeur, étaient négativement corrélées au calcium ($r_s < -0,7$), et étaient inférieures dans l'argile. Quand le niveau de la nappe a monté et a saturé la couche organique, les concentrations de PTD ont augmenté dans les échantillons d'eau composites (couche minérale organique) mais non dans les échantillons discrets (couche minérale), ce qui indique que les concentrations élevées de PTD proviennent de la couche organique proche de la surface. Les concentrations de PTD dans les échantillons composites étaient négativement corrélées à la profondeur de la surface de la nappe ($r_s = -0,6$) et positivement corrélées à la transmissivité ($r_s = 0,7$) et à la concentration de carbone organique dissous ($r_s > 0,6$). Dans la zone tampon riveraine du sous-bassin exploité, les concentrations de PTD dans les échantillons composites baissaient pendant les périodes de fort ruissellement, mais ces valeurs demeuraient plus hautes que celles du sous-bassin inexploité. Toutefois, à cause de la topographie de surface et de la profondeur variable jusqu'aux couches imperméables d'argile, la surface de la nappe était plus haute dans le sous-bassin exploité, particulièrement dans la zone de coupe. Les coefficients d'exportation moyenne quotidienne de PTD étaient comparables dans le sous-bassin inexploité (14 $\mu g \cdot m^{-2}$) et dans le sous-bassin exploité (12 $\mu g \cdot m^{-2}$).

[Traduit par la Rédaction]

Introduction

Forest harvesting can affect P dynamics in subsurface water by potentially increasing water yield, decomposition of the litter, and weathering of soils as well as decreasing P uptake by plants (Fredriksen et al. 1975; Bosch and Hewlett 1982; Nicolson et al. 1982). Several studies report increased P concentrations of soil solutions in the organic layer (fibrous, humus, and litter) after logging, yet observe no detectable change in mineral soil layers (McColl 1978; Stevens et al. 1989; Yanai 1991). Increased runoff following logging could also increase P export as noted in a northern conifer swamp (Devito and Dillon 1993). Hence, more P may accumulate during low runoff and have a higher probability of being flushed from soils during high runoff after logging, increasing P export to adjacent lakes and contributing to eutrophication. Studies on streams have reported increases as well as no change in P concentrations or exports following logging (Nicolson et al. 1982; McClurkin et al. 1985; Martin and Harr 1989; Ahtiainen 1992). These conflicting results may be due to differences in harvest management practices (e.g., site preparation, buffer size) and physio-

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graphic characteristics (e.g., soils, geology, climate, topography, hydrology, vegetation) of the study sites. The use of buffer strips is a management strategy to ameliorate the effects of watershed disturbance (e.g., Barton et al. 1985).

Forest harvesting on the Boreal Plain (defined Strong and Leggat 1992) has increased in the past decade, yet few data are available on the effects of watershed disturbance on P dynamics in this region. Mixedwood forests, covering over 200 000 km^2 on the Boreal Plain, generally have P-rich soils underlain by deep loamy to clay tills (>30 m; Strong and Leggat 1992). In contrast, most studies on the effects of logging have been conducted in regions with P-poor soils and shallow bedrock (<3 m). Riparian buffer strips may reduce P transport from cut blocks through plant uptake of soluble P or entrapment of particulate-bound P (Ahtiainen 1992; Castelle et al. 1994). Recent forest harvesting on the Boreal Plain provided incentive to begin an evaluation of its effects on P dynamics in subsurface waters in areas with deep glacial till.

The objectives of this study are to assess spatial and temporal trends of total dissolved P (TDP) in shallow subsurface water (<2.5 m deep) within 100 m of a boreal lake and the effects of forest harvesting and vegetated buffers on these trends. Since sediment transport, which increases with soil exposure and disturbance, was minimal at the study sites (E.E. Prepas, unpublished data; Ahtiainen 1992), only TDP was analyzed. Shallow subsurface water was sampled because the primary source of P likely to be affected by forest harvesting is the organic layer, and clay and Ca content, which immobilize P, usually increase with depth in boreal soils (Frossard et al. 1989). The hypotheses tested in this study were that TDP concentrations in shallow subsurface water would decrease with depth, increase when the water-table intersected the organic layer, be higher in the cut than in the uncut subcatchment (SC), and decrease across the 23-m buffer strip. In addition, TDP export and export coefficients were hypothesized to be higher from the cut than from the uncut SC.

Material and methods

Study site

This study was part of the Terrestrial and Riparian Organisms, Lakes and Streams (TROLS) project, an interdisciplinary research project based at the University of Alberta. The primary objective of the TROLS study was to determine the effects of forest harvesting practices on various aspects of terrestrial and aquatic ecosystems in the mixedwood forest on the Boreal Plain and what role riparian buffer strips of differing widths play in mitigating potential harvesting effects. This study was conducted in two SCs of Moose Lake (55°09′N, 111°45′W), which had a planned 20-m buffer treatment. The study lake was one of the 12 TROLS study lakes, within the Forest Management Area of Alberta–Pacific Forest Industries, Inc. near the town of Lac La Biche, Alberta, and was designated LLB20 (Fig. 1). The drainage basin area of Moose Lake is 575 ha with a mean slope of 8%. Topography is level to rolling, typical of upland areas of the Boreal Plain. The mean drainage basin slope of Moose Lake at 8% is higher than for the other 11 TROLS lakes (mean 4%, range 1–5%). Soils are predominantly Gray Luvisols and Eutric Brunisols in uplands and Gleysols in lowlands. Primary surficial deposits in the region are undifferentiated Quaternary drift, 100–200 m thick, underlain by shale and siltstone of the Cretaceous–Colorado Group (Tokarsky and Epp 1987).

Table 1. General characteristics of the uncut and cut SCs of Moose Lake.

Characteristic	Uncut	Cut
Area (ha)	5.1	2.7
Mean slope of SC (%)	16	24
Mean slope along transect (draw) (%)	8	11
Range of slope to topographic divide (distance to divide: 20–140 m) (%)	15–30	10–20
% conifer along center transect[a]	33	39
% deciduous along center transect[a]	67	61

Note: [a]For seven plots, each with an area of 9 m^2.

Climate in the Moose Lake region is continental with warm summers (mean July temperature 18°C) and cold winters (mean January temperature −17°C), and evapotranspiration generally exceeds precipitation (Atmospheric Environment Service 1998). Long-term (1971–1997) mean annual precipitation and evapotranspiration, calculated as weighted means of data measured at Atmospheric Environment Service stations in Athabasca, Slave Lake, Fort McMurray, and Cold Lake, were 468 and 514 mm, respectively. Evapotranspiration values were estimated from mean monthly temperatures and day length by Thornthwaite's method (Hewlett 1982), although we recognize that this method is only corrected for sunlight to 50°N. Approximately 50% of the annual precipitation occurs from June to August, and snowfall accounts for another 25–30%. In 1997, during this study, annual precipitation and potential evapotranspiration were 487 and 482 mm, respectively. In 1996, annual precipitation was high, 576 mm, creating high antecedent soil moisture for 1997. Annual discharge of the nearby Owl River was less than 90 $m^3 \cdot year^{-1}$ for each year from 1983 to 1995 and then increased to 185 and 239 $m^3 \cdot year^{-1}$ the year before and the year of the study (1996 and 1997, respectively; Water Survey of Canada 1998). Therefore, this study was conducted during a high runoff period.

The uncut and cut SCs were chosen on the basis of similar aspect, vegetation, and mean slope prior to winter (1996–1997) logging (Table 1). A treed buffer strip with a mean width of 23 m was left along the shore of the cut SC. Forest harvesting was by feller buncher with minimal soil disturbance. The SCs were defined by their topographic boundaries, although some subsurface flow paths originated from outside these boundaries (K.J. Devito, unpublished data). Mean slopes of the transects in the uncut and cut SCs (16 and 24%, respectively) were greater than the mean drainage basin slope for Moose Lake (8%). Percent conifer cover was higher along the transects (33–39%) than in the drainage basin (7%) because the transects were in draws, which tend to have more conifers than the uplands on the Boreal Plain. Although percent conifer cover in the draws was relatively high, it was within the range of percent conifer cover in the TROLS drainage basins (1–42%). Vegetation was typical of the boreal mixedwood forest, comprised of trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white spruce (*Picea mariana*), and some paper birch (*Betula papyrifera*). Willow (*Salix* sp.) and alder (*Alnus* sp.) grew along the shore of the uncut SC. Prior to forest harvesting, an alder stand was prominant at site C9 in the cut SC.

Three main transects, 20–60 m long, of wells and piezometers were installed 4 m apart in the center of the topographic low of both SCs (Figs. 2 and 3); the latter were chosen to enhance the probability of intersecting the water table with shallow wells and piezometers. Wells consisted of 2-m-long polyvinylchloride pipe (Schedule 40, inner diameter 51 mm) with slots (3 mm wide, 24 mm long) every 7.5 cm on either side along the entire length and above the ground surface. Piezometers consisted of solid polyvinylchloride pipe (Schedule 40, inner diameter 19 mm) with a 17.5-cm-long screened end (slots 0.010 mm, 6 mm apart) wrapped

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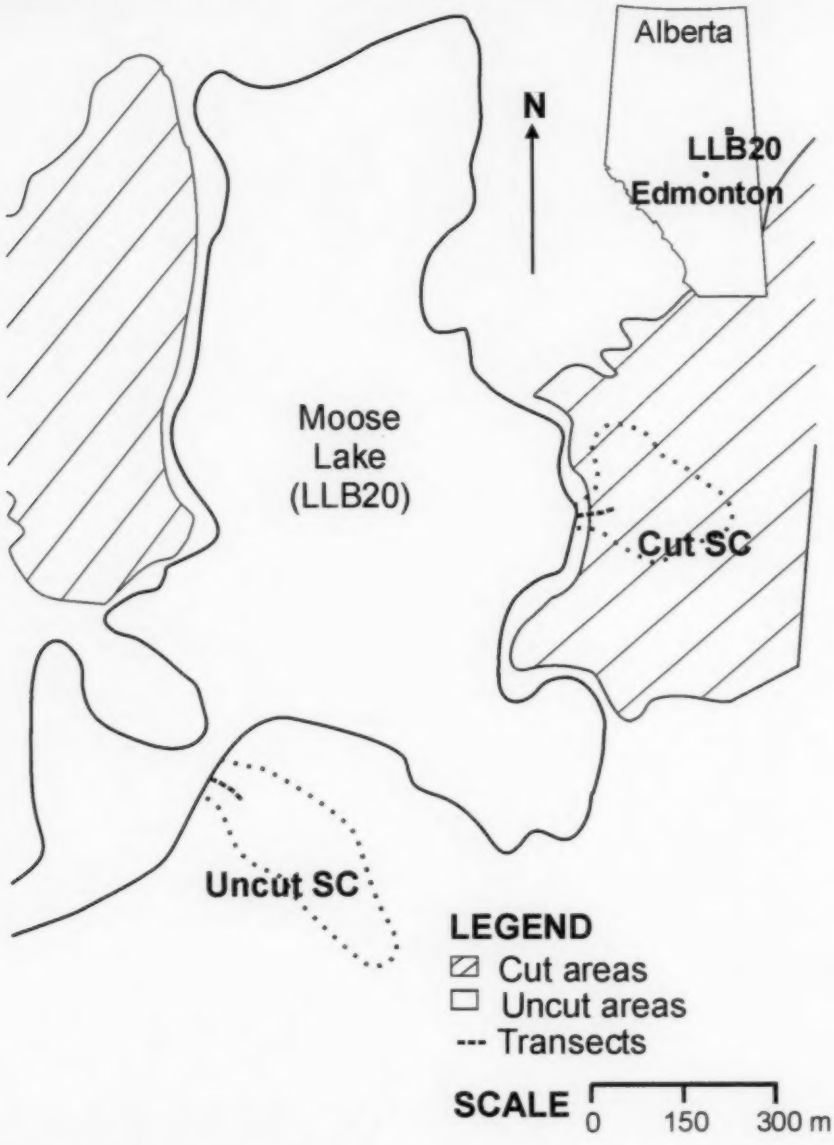
Fig. 1. Location of SCs with transects and distribution of cut blocks at Moose Lake (55°09′N, 111°45′W). The buffer strip is between cut blocks and the lake perimeter.



in spunbond polyester fabric (NILEX MD7407, opening size <100 μm). The sampling sites consisted of nested piezometers and a well, except for the single well closest to the lake in each transect. Wells were 1.1–1.9 m deep. Most piezometers were between 0.9 and 2.5 m deep. Three sites were installed approximately 4 m apart from the first well in all transects. The transects were labelled C or U in the cut and uncut SCs, respectively, and numbered beginning at the lakeshore. In the center transect, four additional sites were installed: three were approximately 4 m apart between 20 and 36 m and one was about 50 m from shore. Topography, wells, and piezometers were surveyed with a total station (Sokkia 3B-II) on October 10, 1997.

Basic soil profiles were recorded while installing the wells and piezometers. Soil texture was interpolated between sites. The organic layer includes leaf litter and fibrous and humic matter. The hand texture method was used to identify general mineral soil textures: loamy sand to sand (S), sandy loams to loams (SL), clay loams to sandy clay (CL), and clay (C) (Steila and Pond 1989).

Field sampling

Wells were sampled approximately every 2 weeks from late March to early October 1997. Piezometers were sampled once in May and approximately every 2 weeks from July to October. Water levels in wells and piezometers were measured prior to purging. Wells and piezometers were purged the day before sampling due to slow recovery rates in several wells and piezometers. Wells were sampled with a Nalgene bailer attached to a stainless steel chain.

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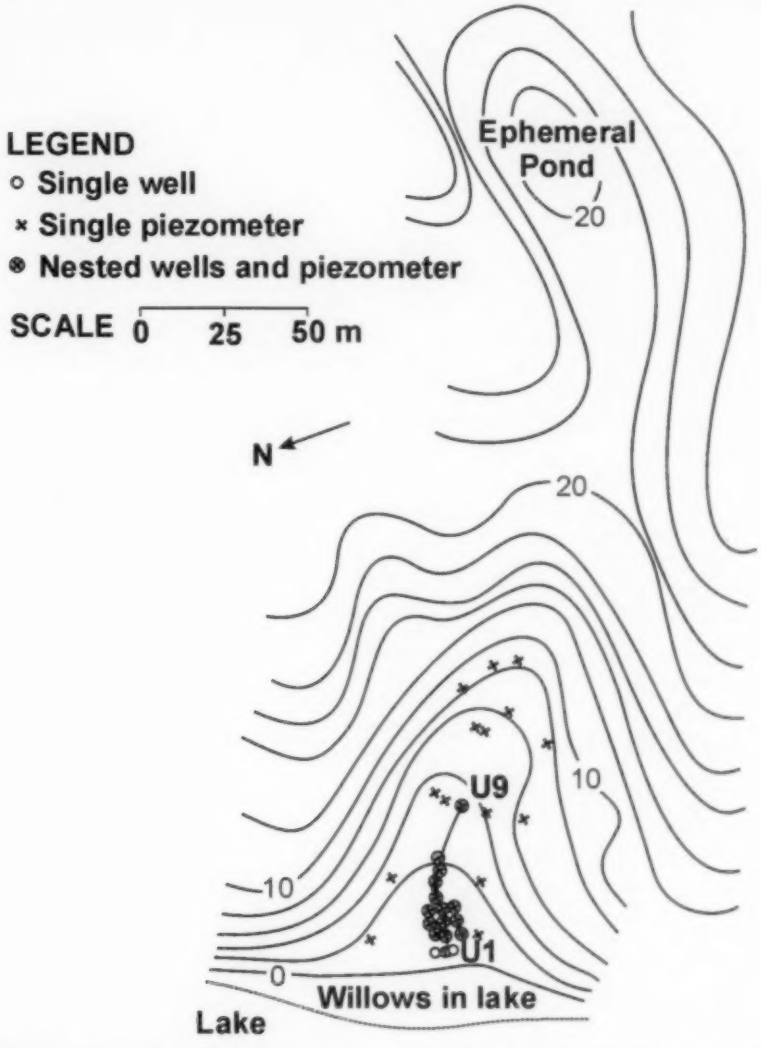
Fig. 2. Well and piezometer sites and topography of the uncut SC. The line ending at U1 and U9 represents the center transect. Contour intervals = 2 m.



Piezometers were sampled with a tube attached to a Nalgene Erlenmeyer flask and hand vacuum pump or to a syringe with a three-way valve. All containers used were acid washed in 10% HCl. Water samples from wells are composite samples of water from organic and mineral soil layers, whereas water samples from piezometers are discrete samples from a mineral soil layer. Water samples were kept on ice for 12–48 h until prepared for analysis.

Physical and chemical analyses of water samples

Temperature, specific conductance, and pH of each sample were determined in the field with ORION model 130 and 250A meters, respectively. All water samples were filtered and prepared in the laboratory within 48 h of collection and then stored at 4°C. Samples were filtered through a prerinsed Gelman glass filter (average pore size 1.2 μm) prior to analysis for dissolved organic C (DOC) and cations and through a prerinsed 0.45-μm Millipore HAWP membrane filter for TDP. DOC concentrations were determined by combustion with an Ionics 1505 programmable C analyzer. Cation samples were acidified to a pH of 3 with nitric acid, and concentrations were measured with a Perkin Elmer 3300 atomic absorption spectrophotometer. TDP was analyzed according to Menzel and Corwin's (1965) potassium persulfate method as modified by Prepas and Rigler (1982). Mean concentration of duplicates was reported for each sample.

Hydrological calculations

Pressure heads and groundwater levels were used to determine the general direction of water flow. Equipotential lines were drawn by hand with the triangulation method (Freeze and Cherry 1979). As a first and tractable calculation of P loading from the SCs, groundwater flow was assumed to be perpendicular to the equipotential lines and soils were isotropic and homogeneous.

Saturated hydraulic conductivities (K_{sat}, metres per day) were determined for each piezometer by Hroslev's method (Fetter 1994). Geometric mean K_{sat} values for each mineral soil type (S, SL, CL, and C) were determined from the K_{sat} values of piezometers. Some

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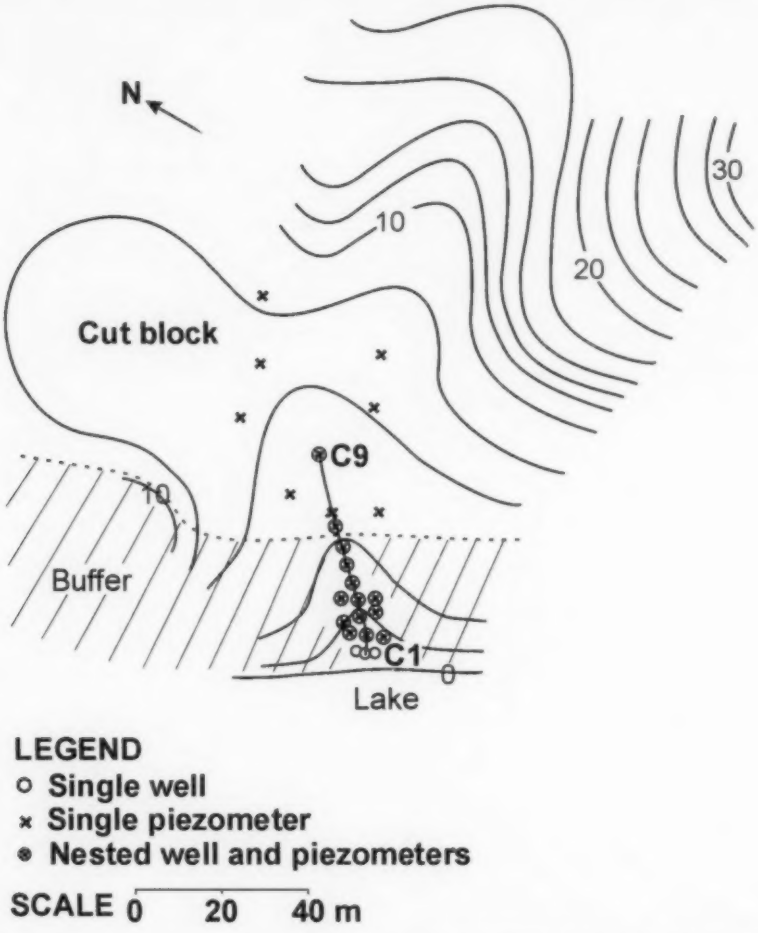
Fig. 3. Well and piezometer sites and topography of the cut SC. The line ending at C1 and C9 represents the center transect. Contour intervals = 2 m.



piezometers in clays had extremely slow recovery rates (>4 days) and recorded K_{sat} values less than 10^{-9} m·day^{-1}.

Total transmissivity (T, square metres per day) of each well was determined for each sampling date:

$$(1) \qquad T = \Sigma(b_{st}K_{st})$$

where b_{st} (metres) is the portion of saturated soil (O, S, SL, CL, and C) intersected by the well and K_{st} (metres per day) is the mean K_{sat} value for the soil type (Fetter 1994). The b_{st} varied with groundwater level. The K_{sat} values of the organic layer were assumed to be 100 m·day^{-1} due to relatively low bulk densities (mean 0.14 ± 0.01 g·cm^{-3}) estimated during soil studies in the Moose Lake catchment (Carmosini 2000).

Estimation of TDP export and export coefficient

For each sampling date from June to September 1997, TDP export and export coefficients from the top 2 m of soil were estimated at the base of the SCs (C2 and U2) (Fig. 4). To calculate discharge along the transects, it was assumed that most of the groundwater flow occurred in the top 2 m of soils over top of the clay layer with a much lower K_{sat} and that the Dupuit–Forchheimer equation could be used to estimate groundwater discharge, that transmissivities and concentrations in the wells at U2 and C2 were representative of water flowing from the SCs, and that flow paths were the same across U2 and C2. The 2-m depth limit likely resulted in an underestimate of flow, while the assumption of similar flow paths across U2 and C2 resulted in an upper limit on the estimate. TDP exports (milligrams per day) were estimated by taking the sum of the product of the hydraulic gradient (dh/dx), mean TDP concentration (C, milligrams per cubic metre), and transmissivity (T, square metres per day) for the wells and width (d, metres) of draws at U2 or C2:

$$(2) \qquad \text{Export} = (dh/dx)CTd.$$

Hydraulic gradient was estimated from wells above and at U2 and C2. The widths, delineated from substantive breaks in slope on either side of U2 and C2, were 35 and 22 m, respectively. TDP export coefficients (micrograms per square metre per day) were estimated from daily export (micrograms per day) divided by SC area (square metres).

Statistical analyses

Samples from wells and piezometers in each SC were considered as separate groups because discrete samples from mineral soil

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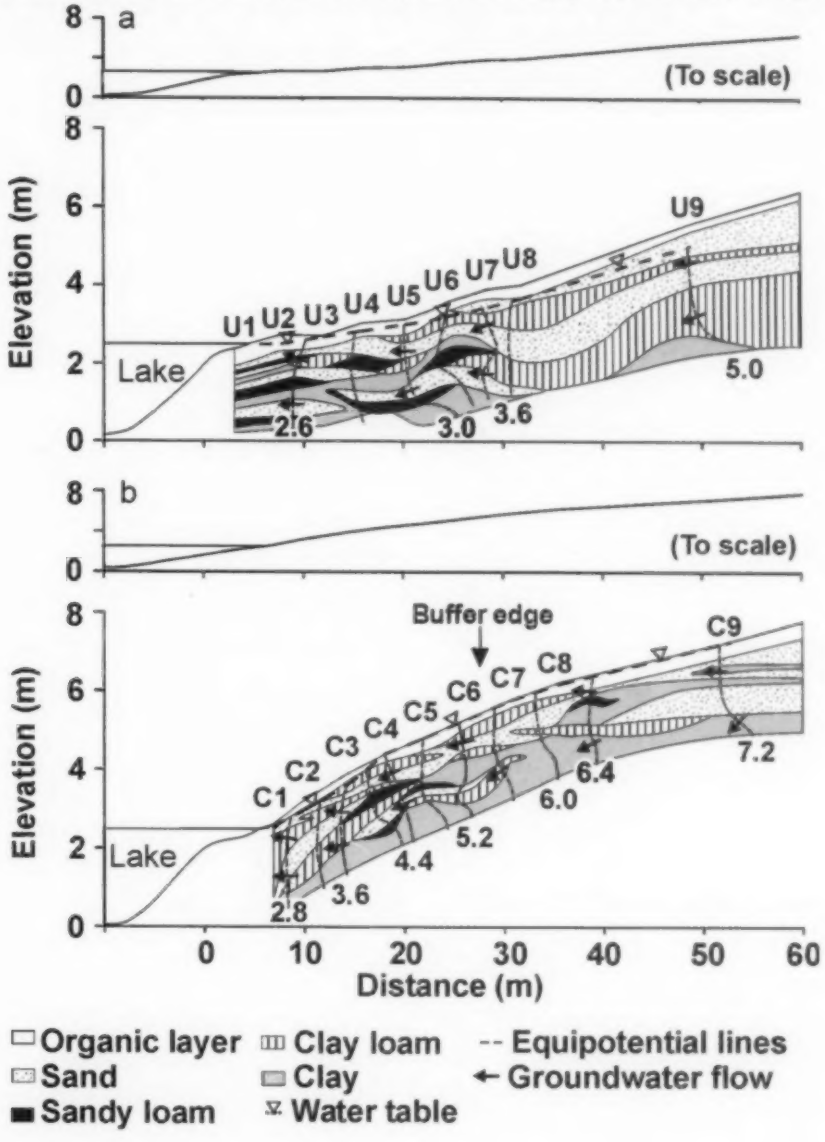
Fig. 4. Subsurface flow during high runoff (June 15, 1997) and general soil texture along the center transect of the (*a*) uncut and (*b*) cut SCs. Numbers are head or level (m). The top part of each panel shows the slope and lake with no vertical exaggeration.



layers were collected from piezometers, and composite samples from organic and mineral soil layers were collected from wells. Spearman's rank correlation coefficient (r_s) and the Mann–Whitney test were used because the data did not meet the assumptions of normality and homogeneity of variance. Scatterplots and r_s were used to find trends among the measured parameters. Levels of significance for r_s between TDP and other parameters were adjusted by Bonferroni's equation to account for multiple parameters tested. Since Ca and Mg were strongly correlated ($r_s > 0.95$, $P < 0.001$), as would be expected in carbonate-rich soils, correlations with Ca, but not with Mg, were included. The Mann–Whitney test was used to determine differences in mean TDP concentrations between the uncut and cut SCs and between shallow and deep piezometers. Statistical tests follow Snedecor and Cochran (1989).

Results

Soil texture and hydrology

The surficial soil texture consisted of interlayers of sand and clay glacial till in both SCs (Fig. 4). These layers were often discontinuous, leading to considerable spatial variability. The organic layer in the uplands of the cut SC (C9: 39 cm) was almost double the thickness of the uncut SC

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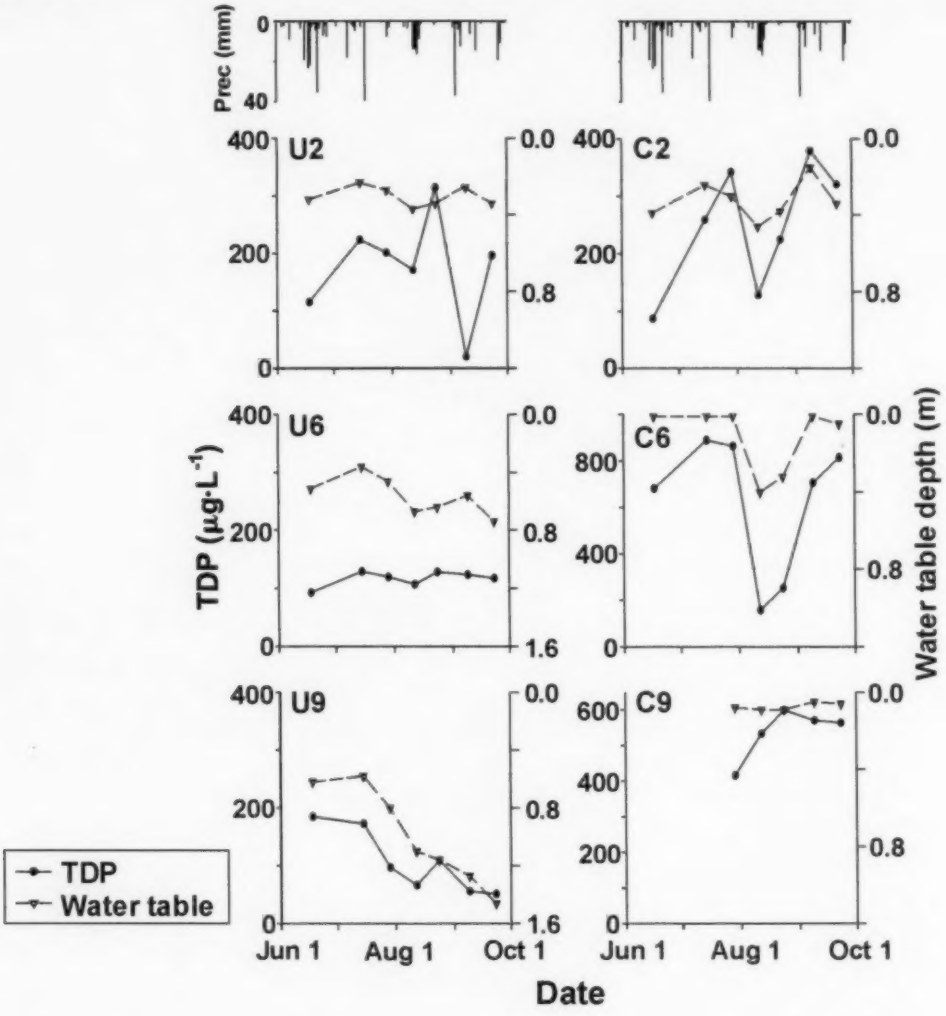
Fig. 5. Precipitation, water table (solid circles) depth relative to ground surface, and TDP concentrations (triangles) at U2 and C2, U6 and C6, and U9 and C9.



(U9: 20 cm). Near the lake, the organic layer of the cut SC (C1: 25 cm) was less than half the thickness of the uncut SC (U1: 61 cm). Both SCs had a large sandy layer in the uplands and many interlayers of sand and clay till near the shore. The upper soil layers in the cut SC were underlain by a shallow (1–2 m deep) broad layer of clay, whereas a deeper clay layer occurred in the uncut SC.

Mean hydraulic conductivities (and range) of the mineral soil layers were sand 1.8 (1.3–3.0), silty sand 9.2×10^{-2} (1.0×10^{-2} to 9.8×10^{-1}), sandy clay 1.1×10^{-3} (1.4×10^{-4} to 8.5×10^{-3}), and clay 7.7×10^{-6} (9.0×10^{-8} to 9.2×10^{-8}) m·day^{-1}. These are within the range for K_{sat} values of similar soil types stated in the literature (Fetter 1994). Since the K_{sat} values of the organic layer were estimated to be much higher than those of mineral soil layers, mean transmissivity of wells where the water table intersected the organic layer (14 ± 1.3 m^2·day^{-1}) was two orders of magnitude higher than that of wells where the water table was below the organic layer (0.11 ± 0.033 m^2·day^{-1}).

Although lateral flow dominated both sites from June through October 1997, the two SCs had different groundwater table profiles (Fig. 4). Although subsurface flow during high flow is shown in Fig. 4, flow was similar throughout the study period. Mean water table depth in the uplands (U9) of the uncut SC was approximately 1 m below the surface and became shallower approaching the lake (U2: mean depth 0.30 ± 0.03 m) (Fig. 5). In contrast, mean water table depth (0.04 ± 0.01 m) was consistently high in the uplands (C9) of the cut SC, fluctuating only 7 cm from June to September 1997. Although no data are available for 1996, this area supported alders, which suggests that soil conditions were often saturated prior to logging. Mean water table depth usually

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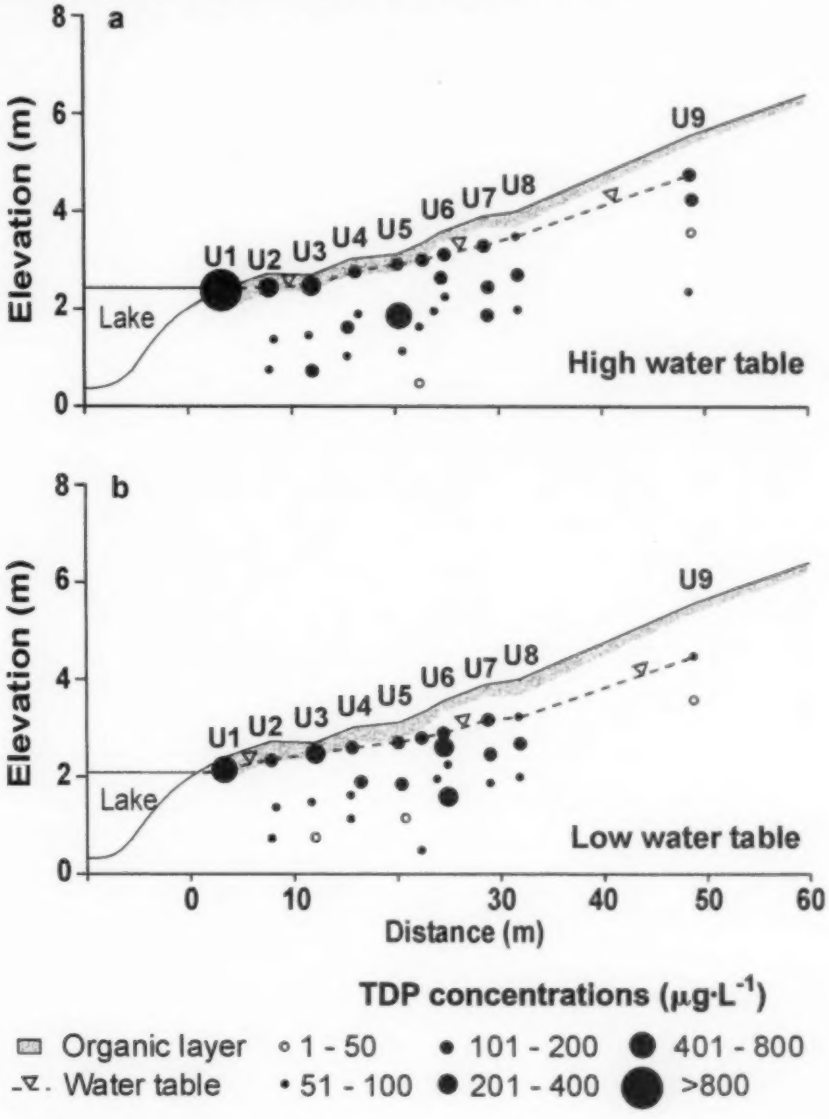
Fig. 6. TDP concentrations in piezometers and wells (circles on the water table) along the center transect of the uncut SC when the groundwater table was (*a*) high (July 29, 1997) and (*b*) low (August 12, 1997).



remained high at C6 (mean depth 0.03 ± 0.06 m) and became deeper approaching the lake (C2: mean depth 0.31 ± 0.04 m). Water table fluctuations were dynamic; for example, they dropped between 14 and 76 cm at all the sites (excluding C9) within a 4-week period (July 15 to August 12, 1997) (Fig. 5).

Trends along the hillslope

TDP concentrations in piezometers generally decreased with depth (Figs. 6 and 7). TDP concentrations in most wells were higher than, or similar to, concentrations in adjacent piezometers. Furthermore, mean TDP concentrations in both SCs were higher in piezometers above, than in those below, a depth of 1.7 m ($P < 0.01$). The lowest TDP concentrations were usually for piezometers in clay. In addition, TDP and Ca concentrations were negatively correlated in piezometers ($r_s > 0.7$, $P < 0.001$) (Fig. 8). Calcium concentrations in piezometers generally decreased with depth.

TDP concentrations in wells generally increased after summer rainstorms when the water table rose and intersected the organic layer, while concentrations in most piezometers remained relatively similar (Figs. 5, 6, and 7). However, TDP concentrations were also high in the wells from C2 to C4 when the water table was below the organic layer. Water from the organic layer near C5 may have flowed along the adjoining sandy layer to the wells at C2–C4 (Fig. 4). TDP

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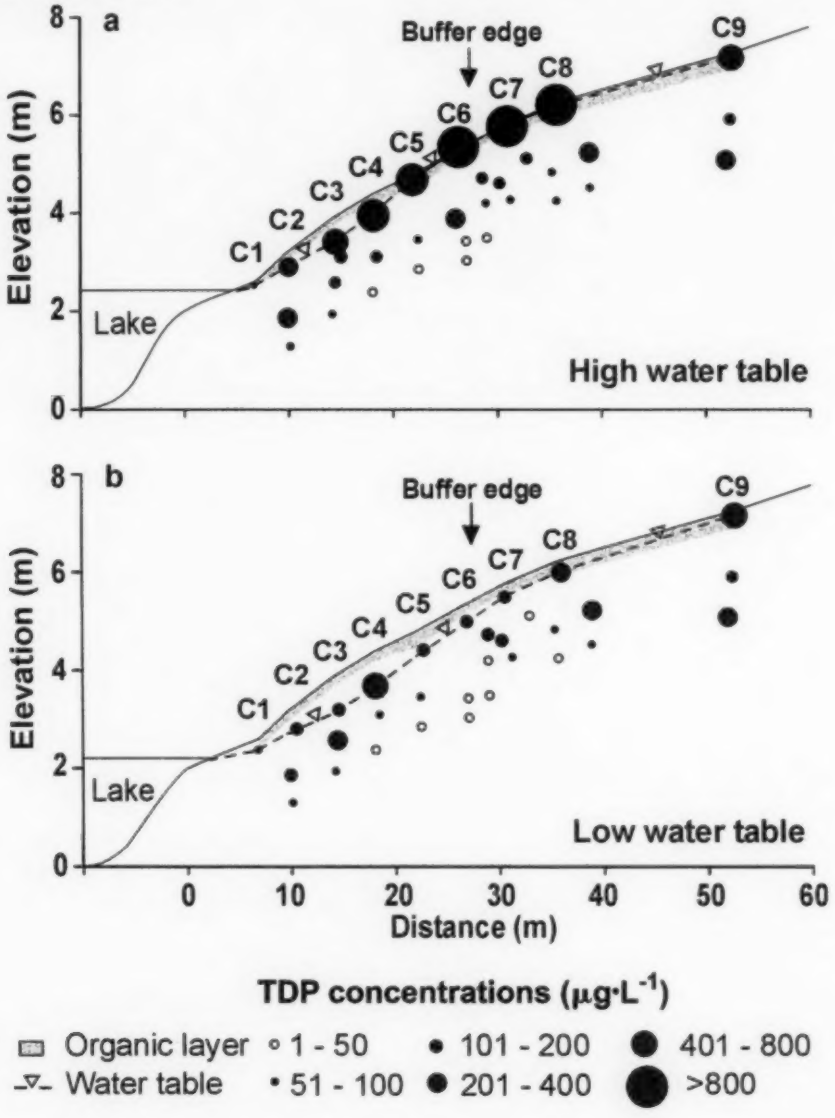
Fig. 7. TDP concentrations in piezometers and wells (circles on the water table) along the center transect of the cut SC when the groundwater table was (*a*) high and (*b*) low.



concentrations in wells were negatively correlated with water table depth ($r_s = -0.6$, $P < 0.001$) and positively correlated with transmissivity ($r_s = 0.7$, $P < 0.001$), DOC ($r_s > 0.5$, $P < 0.001$), and K ($r_s > 0.4$, $P < 0.001$) (Fig. 9). There were apparent thresholds around 0.4 m for water table depth and 60 mg C·L^{-1} for DOC below which there was no relationship with TDP concentrations. In the mineral soil layers (piezometers), there was no identifiable relationship between TDP and DOC concentrations, which were mostly less than 60 mg C·L^{-1} (Fig. 8). Thus, TDP concentrations in wells, which may receive water from both mineral soil and organic layers, were related to DOC, K, and transmissivity, while TDP concentrations in water from only the mineral soil layers were not related to DOC, K, or K_{sat}.

TDP concentrations in wells were two to eight times higher in the cut SC than in wells further than 23 m from shore in the uncut SC ($P < 0.05$) (Figs. 6 and 7). The difference between TDP concentrations was greatest when the water table was high. Shallow piezometers (<1.7 m deep) had similar mean TDP concentrations in the two SCs ($P = 0.96$). Mean TDP concentration in deeper piezometers (>1.7 m deep) was about 1.5 times (46 μg·L^{-1}) higher in the uncut than in the cut SC ($P < 0.05$). In the buffer strip, except at C4, which had a higher concentration, TDP concentrations

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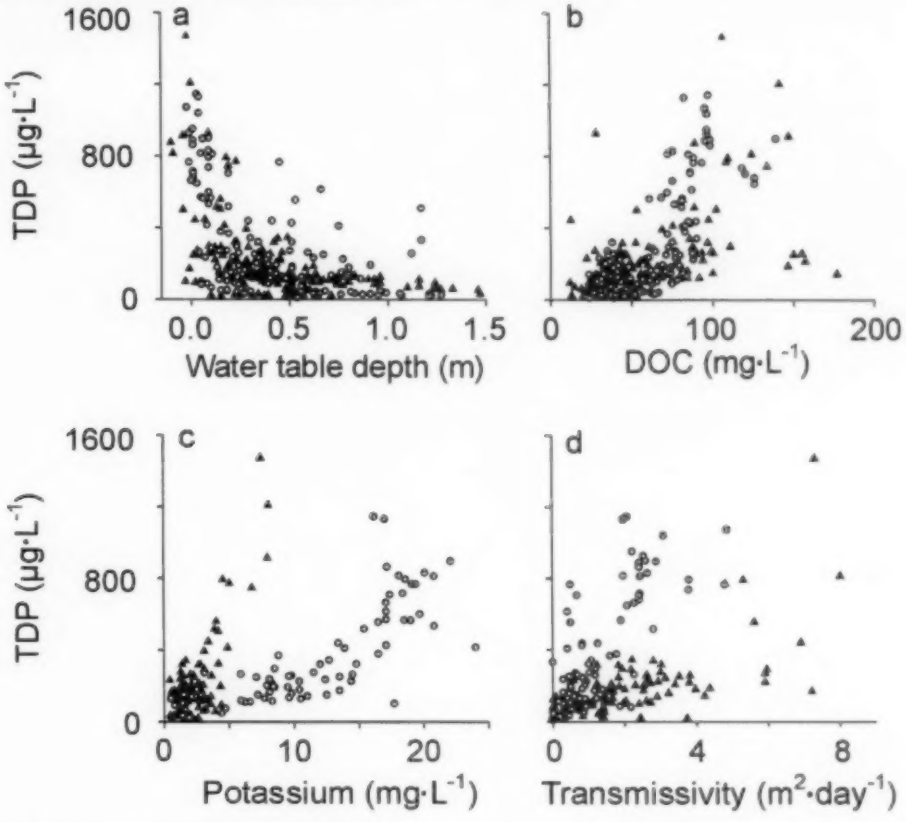
Fig. 8. Relationships between TDP concentrations in wells and (*a*) water table depth below ground, (*b*) DOC, (*c*) K, and (*d*) transmissivity for cut SC (circles) and uncut SCs (triangles).



were similar (100–200 µg·L^{-1}) from C7 to C2 when the water table was below the organic layer (Fig. 7*b*). However, when the water table was high, TDP concentrations in wells decreased by an order of magnitude with distance from the cut block into the buffer, although the water table dropped at the same time (Fig. 7*a*). In contrast with TDP concentrations, estimated mean daily TDP export was higher in the uncut SC (728 ± 881 mg) than in the cut SC (431 ± 370 mg); however, estimated daily TDP export coefficients were similar in both SCs (uncut: 14 ± 17 µg·m^{-2}; cut: 11 ± 2 µg·m^{-2}) (Table 2).

Discussion

Influence of mineral soil characteristics

Consistent with our first hypothesis, TDP concentrations decrease with depth in the mineral layer. This decreased concentration was likely due to a combination of increased soil content of Ca, clay, and perhaps Fe (not measured), as phosphates react with Ca, Fe, and clay particles to form relatively insoluble compounds (Cresser et al. 1993). In similar soils in northern Saskatchewan, precipitation of calcium phosphates increased with depth (Frossard et al. 1989). As suggested in other studies (Sharpley 1983; Frossard et al. 1989), the negative correlation between TDP and Ca concentrations in piezometers suggests that Ca limited P solubility, and thus mobility, in mineral soil layers of the study hillslopes. In our study, mean TDP concentrations were highest in shallow piezometers (<1.7 m deep), which were in soils with less clay, supporting the idea that clay limits P mobility. Calcium, clay, and Fe can be important in decreasing P solubility with depth in forested soils on the Boreal Plain.

Influence of organic matter and water flow

Consistent with our second hypothesis, TDP concentrations, and thus P mobility, increased when water flowed through the organic layer. The positive correlations among K, DOC, and TDP concentrations suggest that water from the organic layer had higher TDP concentrations than mineral soil layers, as the organic layer is the most likely source of both DOC and K in subsurface water (Chapman et al. 1993; Boyer et al. 1996). Phosphates are also more mobile in organic-rich soils because organic matter has a low affinity for binding phosphates (Huang and Schoenau 1997) and competes with P for adsorption sites on mineral colloids (Singh and Jones 1976). Therefore, water contributed to wells from the organic layer likely had higher TDP concentrations.

Several studies have developed models in which DOC or

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Fig. 9. Relationships between TDP concentrations in piezometers and (*a*) DOC and (*b*) Ca for cut (circles) and uncut SCs (triangles).

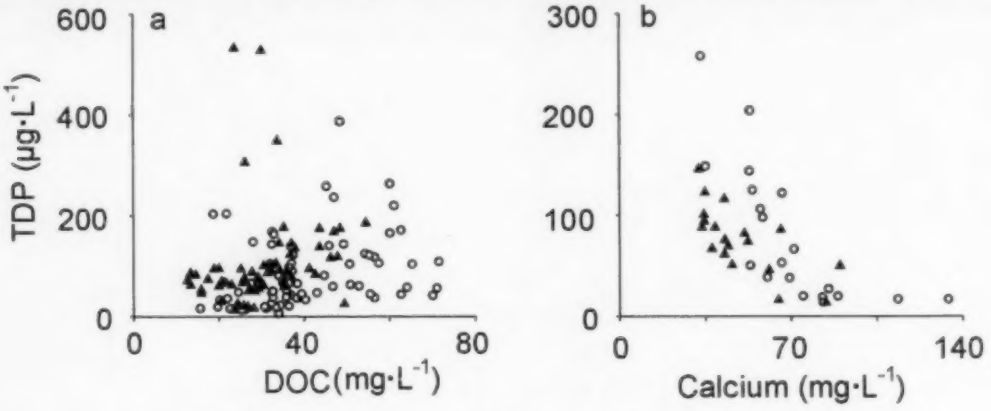

Table 2. Estimated daily P export and export coefficient in the cut and uncut SCs from June to September 1997.

	Cut		Uncut	
Date	Export (mg)	Coefficient (µg·m^{-2}·day^{-1})	Export (mg)	Coefficient (µg·m^{-2}·day^{-1})
June 18, 1997	263	10	1588	31
July 15, 1997	563	21	6933	135
July 29, 1997	509	19	2403	47
August 12, 1997	142	5	7	0.1
August 24, 1997	255	9	702	14
September 9, 1997	2908	11	1185	23
September 23, 1997	350	13	705	14
Daily mean	431	12	722	14
SE	370	2	881	17

nitrate accumulated in the organic layer during low-flow periods and was flushed from the soil during high flow (Boyer et al. 1996; Creed et al. 1996). This flushing concept is useful in explaining spatial and temporal patterns in TDP concentrations in the boreal mixedwood forest. TDP concentrations in wells increased in both SCs during high runoff as the water table approached the ground surface (water table depth = 0 m) and transmissivity increased. When the water table rose and intersected the organic layer, P that had accumulated while the organic layer was relatively dry was likely flushed out and increased TDP concentrations in our wells. However, TDP concentrations in wells from C7 to C2 were still relatively high when the water table was low and below the organic layer. These concentrations were likely maintained by water flowing from the organic layer in the cut block via the sandy layer to the wells. Therefore, TDP concentrations in wells were higher during high flow, suggesting that subsurface flow flushed P from the upper soil layers, as reported in other studies for a range of nutrients.

Influence of structure and topography

Lithology and topography influenced subsurface flow and thus TDP concentrations in our wells. The shallow clay lenses, underlying soil layers with higher K_{sat} values, caused lateral subsurface flow to occur in the top 2 m of soil. Further, water likely flowed over the shallow clay lenses, contributing to the high water table from C5 to C9 in the cut SC and near the shore in the uncut SC, thereby increasing water flow through the organic layer and thus TDP concentrations in our wells. TDP concentrations were usually higher in areas with lower slopes (i.e., from C5 to C9 in the cut SC and near the shore in the uncut SC), supporting a study of 30 Canadian Shield lakes that found that total P was negatively related to catchment slope (D'Arcy and Carignan 1997). The low, concave slopes around C9 and near the shore in the uncut SC also likely contributed to the thick accumulation of organic matter at U1 (61 cm) and at C9 (39 cm), as nutrients, soil, and water tend to accumulate in depressional areas (Anderson 1987). Water from the organic layer in the cut block likely flowed along the sandy layer into the wells from C7 to C2 and maintained the relatively high TDP concentrations (>120 µg·L^{-1}), even during low flow. Therefore, TDP concentrations in wells were usually higher in areas with the lowest slope (C9 and U1) and likely influenced TDP concentrations in areas downslope from them.

Influence of forest harvesting

TDP concentrations in piezometers (mineral soil) were not likely influenced by forest harvesting. Several studies observed that TDP concentrations in a solution of mineral soils were similar before and after logging, probably due to

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high P adsorption capacity of the soils (e.g., McColl 1978; Yanai 1991). In our study, mean TDP concentrations in piezometers less than 1.7 m deep were not detectably different between the SCs. However, mean TDP concentrations in piezometers deeper than 1.7 m were lower in the cut SC ($P < 0.05$). Variation in TDP concentrations in piezometers was likely due to higher clay content in soils of the cut SC rather than to a logging effect.

Except at U1 and C1, TDP concentrations in wells were higher in the cut SC than in the uncut SC. However, the difference between TDP concentrations between the two SCs was likely due to differences in their hydrology and not to the direct effects of logging as hypothesized. Water intersected the organic layer more often in the cut SC, likely flushing out P and thus increasing TDP concentrations in wells. Furthermore, this study was conducted during a period of extremely high runoff because 1996 had the second highest precipitation in 27 years. Thus, antecedent soil moisture was high at the beginning of our study, creating a high potential for water to flush P from the organic layer. Nonetheless, forest harvesting often increases water yield due to decreased interception and evapotranspiration and increased soil moisture (Bosch and Hewlett 1982) and could have contributed to the rise in the water table of the cut SC. If water yield increases enough to raise the water table to the surface after logging on the Boreal Plain, the potential for P export to lakes will increase, especially from low-lying areas, where the water table is naturally close to the surface during wet years. Thus, differences between the uncut and cut SCs could not be attributed to logging because of differences in soil texture, which influences the hydrology.

TDP concentrations in wells decreased with distance into the buffer strip when the water table was high and flowed through the organic layer. This appears to be due to the deeper water table with distance into the buffer, dropping below the organic layer, and likely influenced TDP concentrations. When the water table was low and below the organic layer, TDP concentrations were relatively similar at five of six sites through the buffer strip. Although subsurface water flowed through the rooting zone, TDP concentrations increased when water flowed through the organic layer, which includes both the litter and the humus layer. In a study in northern Saskatchewan, P uptake by plants was greatest in the humus layer where fine roots were concentrated (Huang and Schoenau 1996). Since TDP concentrations decreased in the buffer only when the water table fell below the organic layer, the organic layer was likely a greater source of P than plant uptake was a sink for P. Therefore, in this short-term study, the buffer strip did not appear to reduce TDP concentrations, although longer-term studies would clarify the issue.

Contrary to our hypothesis, estimated mean daily TDP export was higher from the uncut SC than from the cut SC, and estimated mean daily TDP export coefficients were similar from both SCs (uncut, 14 $\mu g \cdot m^{-2} \cdot day^{-1}$; cut, 12 $\mu g \cdot m^{-2} \cdot day^{-1}$). Estimated mean daily TDP coefficients were similar to mean daily export coefficients for streams in conifer-dominated (19 $\mu g \cdot m^{-2} \cdot day^{-1}$; Munn and Prepas 1986) and in aspen-dominated watersheds (27 $\mu g \cdot m^{-2} \cdot day^{-1}$; Cooke and Prepas 1998) on the Boreal Plain. Phosphorus export coefficients based on weekly samples underestimate those based on daily samples (Munn and Prepas 1986). Since our samples were collected twice monthly, P export coefficients were likely seriously underestimated, more than compensating for the two-dimensional models used to estimate these coefficients in our study. Further, the period immediately after the major storm event at the end of June 1997, when TDP export was likely at its highest, was missed. Estimated daily export coefficients of the subsurface flow and streams on the Boreal Plain were within a similar range, suggesting that subsurface water plays an important role in TDP exports in streams.

Studies need to be done on P transport from areas of the boreal mixedwood forest with different physiographic features (e.g., concave and convex slopes, lowlands and uplands, wetlands), with and without disturbances, to understand how to minimize P export to lakes and streams. For studies of soil nutrient cycles on the Boreal Plain, multiple-year studies are required to integrate the effect of climate and forest harvesting.

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Forest fire induced impacts on phosphorus, nitrogen, and chlorophyll *a* concentrations in boreal subarctic lakes of northern Alberta

P. McEachern, E.E. Prepas, J.J. Gibson, and W.P. Dinsmore

Abstract: The biogeochemistry of 10 headwater lakes in burnt peatland–conifer catchments and 14 in unburnt catchments was evaluated throughout a summer 2 years following forest fire in a boreal subarctic region of northern Alberta. Cation exchange within burnt catchments resulted in proton flux and a 9% reduction in mean pH. Lakes in burnt catchments contained more than twofold higher ($P << 0.01$) mean concentrations of total, total dissolved, and soluble reactive phosphorus, 1.5-fold higher ($P << 0.01$) concentrations of dissolved organic carbon, and more than 1.2-fold higher ($P < 0.05$) concentrations of total and total dissolved nitrogen, nitrate + nitrite, and ammonium compared with reference lakes. Total phosphorus concentration explained 86% of the variance in reference lake chlorophyll concentration but was not related to chlorophyll concentration in burnt lakes. Analysis of chlorophyll – total phosphorus residuals suggested that algae in burn-impacted lakes were light limited. With the addition of five lakes burnt between 1961 and 1985, time since disturbance and percent disturbance combined explained 74% of the variance in total phosphorus among burnt lakes. Fire caused increased flux of materials to the study lakes with slow recovery over decades.

Résumé : Nous avons étudié la biogéochimie de 10 lacs de tête situés dans des bassins incendiés de tourbières et de conifères, et de 14 dans des bassins non incendiés, tout au long d'un été deux ans après un feu de forêt survenu dans une région boréale subarctique du nord de l'Alberta. L'échange cationique dans les bassins incendiés occasionnait un flux de protons et une réduction de 9% du pH moyen. Les lacs des bassins incendiés présentaient des concentrations moyennes plus de 2 fois supérieures ($P << 0{,}01$) de phosphore total, de phosphore dissous total et de phosphore réactif soluble, des concentrations 1,5 fois supérieures de carbone organique ($P << 0{,}01$) et des concentrations plus de 1,2 fois supérieures ($P < 0{,}05$) d'azote total et d'azote dissous total, de nitrate/nitrite et d'ammonium par rapport aux lacs témoins. La concentration de phosphore total (PT) expliquait 86% de la variance de la concentration de chlorophylle (CHL) dans les lacs témoins, mais n'était pas reliée à la CHL dans les lacs des bassins incendiés. L'analyse des concentrations résiduelles de CHL–PT semble indiquer que les algues des lacs touchés par l'incendie subissaient une réduction de l'éclairement. Si l'on ajoute les données sur 5 lacs de zones incendiées entre 1961 et 1985, la durée écoulée depuis l'incendie et le pourcentage de perturbation combinés expliquent 74% de la variance du PT entre les lacs des bassins incendiés. Le feu causait une augmentation de l'apport de matériaux dans les lacs étudiés, dont le rétablissement va être lent et s'étaler sur des décennies.

[Traduit par la Rédaction]

Introduction

Interest in fire as a natural disturbance impacting catchment biogeochemistry and surface water quality is rekindling as a relative benchmark for anthropogenic impacts. However, studies on the effects of fire on water quality suggest that impacts are regionally or fire specific due to organic soil characteristics, severity of fire, and hydrologic regime. The magnitude of ion flux from catchments is thought to depend on fire severity because of modifications to cation exchange and biochemical reactions in the organic soil layer (Grier 1975; Stark 1977; Schindler et al. 1980). In experimental fires where a third or less of the organic soil layer was burnt, no detectable changes in soil water and stream water carbon, nitrogen, phosphorus, their inorganic fractions, or major cations were reported (e.g., Richter et al. 1982). Following more severe fires, increases in nutrient flux were large but usually short-lived (<5 years), and changes in surface water concentrations did not exceed interannual variation (McColl and Grigal 1975; Bayley et al. 1992; Minshall et al. 1997). These studies occurred primarily in regions with thin organic soils, whereas studies in burnt permafrost–peatland dominated systems such as those in northern Alberta are rare.

Water chemistry has been studied in burnt catchments with small proportions of peatlands. A comparison of burnt and unburnt portions of a *Sphagnum fallax* – black spruce (*Picea mariana*) mire demonstrated no detectable long-term (8 years) impact of fire on water chemistry (Vitt and Bayley 1984). In a review of circumpolar studies, MacLean et al. (1983) reported that fire rarely burnt the entire organic layer and changes in soil water chemistry did not result in nutrient

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flux from peat-derived soils. However, wetland catchments had elevated phosphorus flux after severe fires (Bayley et al. 1992). The previous studies give little indication of potential impacts from forest fire in catchments with deep peat soils (0.5 m or more), underlain by glacial till and containing permafrost or seasonal frost lasting a majority of the summer. A lack of data makes it difficult to address the potential impacts of large-scale forest disturbance proposed for catchments of northern Alberta, particularly those containing permafrost where forestry and petroleum activities are increasing.

A unique opportunity to examine extensive damage to peatlands was provided when 129 000 ha of the Caribou Mountains, a subarctic plateau, were razed by fire in 1995. In this single event, one third of the plateau was burnt, equaling 50% of the mean annual area burnt in the province of Alberta between 1994 and 1998 (Alberta Environment, unpublished data). Impacts on lake water chemistry were expected because of high fire severity, a large proportion of catchments burnt (between 60 and 100%), and hydrology dominated by flow through peatlands. We hypothesized that the 1995 fire in the Caribou Mountains would reduce the base cation exchange capacity of peat and increase mineralization of nutrients to produce (*i*) increased base cation and nutrient concentrations in surface waters, (*ii*) corresponding increases in phytoplankton biomass, and (*iii*) increased suspended organic and inorganic seston. We also examined long-term (decades) impacts from fire and relationships between catchment characteristics and lake water chemistry.

Materials and methods

The Caribou Mountains (59°N, 115°W) in Alberta, Canada, are an erosional remnant forming a large, relatively flat plateau 500 m above the Peace River valley. Peatlands cover 56% of the Caribou Mountains and are predominately underlain by poorly drained cryosolic and brunisolic soils (Strong and Leggat 1992). Subsurface geology is shale, feldspathic sandstone, and siltstone of deltaic and marine origin. Open forest of black spruce and an understory of mixed *Sphagnum* spp., feathermosses, brown mosses, and lichens dominate the vegetation. Prior to the 1995 fire, most spruce stands in burnt and reference catchments originated between 1860 and 1910 (Alberta Vegetation Inventory 1 : 20 000 map series, 1983), indicating that there had not been a stand-replacing fire in 90 years. Trembling aspen (*Populus tremuloides*) is concentrated in upland areas. Mean percent upland per catchment is less than 30% but is 83% in one burnt catchment (Table 1). Permafrost is estimated to be between 0.5 and 0.75 m beneath the organic soil surface within continental bogs (Strong and Leggat 1992), which cover an average of 62% of the study catchments. Collapse scars signify degraded permafrost (Vitt et al. 1994) and were present in bogs averaging an additional 19% of the study catchments prior to the fire. In the fire, understory herbaceous, sedge, and lichen cover were incinerated but damage to moss and peat varied. Impact from burning was mostly limited to 0–20 cm of peat. In some locations, burning continued within deeper peat until the following summer. Late August testing in five catchments revealed no permafrost in the peat layer (down to mineral soil) of burnt areas, whereas it was present in five unburnt continental bogs. Mean May–August temperatures were 10.2°C (automated climate station), typically with less than 800 growing degree-days and between 400 and 450 mm of annual precipitation (Strong and Leggat 1992).

Ten headwater lakes were selected with catchments where between 50 and 100% of the tree cover was killed by fire (mean 83%, median 90%, SD 15%). These, plus 14 headwater lakes in unburnt reference catchments and five headwater lakes in catchments burnt between 1961 and 1985, were sampled monthly after ice-out from late June to late August – early September (Fig. 1). The lakes selected from previously burnt catchments were used in time since disturbance and percent disturbance analyses only. Among all combined lakes, differences in surface elevation were less than 90 m across the 120-km distance of this study on the plateau. The study lakes had zero to three neighbours within 20 km contributing the same drainage. Lakes within each of these drainage groups were within 15 m surface elevation of their neighbours. Lake surface areas ranged from 2.6 to 1173 ha and mean depths from 0.3 to 11.6 m. All lakes were either polymictic or, if stratification was observed (late July for deeper lakes), mixed conditions were restored by the next sampling event (August–September). In all lakes, dissolved oxygen concentrations exceeded 5 $mg \cdot L^{-1}$ 0.5 m above the bottom through the summer. Three stream, four fen, and six bog sites were also sampled during the summer of 1997. Two streams, MS1 and MS2, drained adjacent unburnt watersheds of 40 and 6 km^2, respectively. MS3 drained a 1-km^2 watershed that was entirely burnt. Thus, the watershed ratios were 40:6:1 for the three streams. MS2 was gauged for discharge calculations. Samples were collected from MS1, MS2, and MS3 on the same four sample dates, which included bankfull and baseflow conditions. Our limited data show that the ratio of discharge from MS3 relative to the reference streams was 20:1.5:1. Based on this limited data set, the burnt catchment, MS3, released between two- and four-fold more catchment-weighted discharge than the two unburnt catchments.

Ground cover in each catchment was classified as upland–aspen, peatland, or open water. Peatlands were subdivided into veneer bog, peat plateau, poor fen, and rich fen based on vegetation and slope characteristics identified from 1994 1 : 20 000 aerial photographs (Halsey et al. 1997). Percentage of fire disturbance per drainage basin was estimated from 1996 aerial photographs. Bathymetric maps were constructed from depth measurements along 5–15 transects on each lake. Depth measurements were recorded by echosounding at equal time intervals along transects while traveling at a constant velocity and used to interpolate depth contours with ArcInfo. Catchment slope was calculated by computing elevation gain divided by linear distance to lakeshore (CS1: D'Arcy and Carignan 1997) with 10–30 transects from topographic high points and intermediate saddles around the watershed.

At the deepest site in each lake, water temperature and dissolved oxygen (YSI 50B) and light penetration (LI-COR LI-185 and LI-192SB flat sensors) profiles were recorded at 0.5-m intervals. Transparency was estimated with a 20-cm Secchi disc. A 12-L euphotic zone composite water sample was collected with multiple hauls of a polyvinyl chloride tube to the depth of 1% light penetration or 1 m above the lake bottom. Three opaque 2-L acid-washed polyethylene bottles were rinsed and filled with the composite sample. pH of the composite sample was measured with a Hanna HI9025 meter calibrated before each use.

Triplicate 25-mL aliquots were pipetted into 30-mL glass tubes used directly in digestion processes for total and dissolved nitrogen (TN, DN) and phosphorus (TP, DP) analysis. Unfiltered water was used for TN, TP, and ammonium (NH_4^+-N) analyses. Filtrate (Millipore HA, 45 μm) was used for DN, DP, and nitrate + nitrite (NO_3^--N) analyses. TN and DN samples were preserved with 10 μL of 40% H_2SO_4 for storage (1–2 weeks) and neutralized with equivalent NaOH prior to digestion in the laboratory. TP and DP were analyzed spectroscopically (5-cm cell) from persulfate-oxidized samples by molybdate blue absorption (Prepas and Rigler 1982). TN and DN concentrations were determined by second-derivative spectroscopic analysis of persulfate-oxidized samples (Crumpton et

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Table 1. Physical parameters for the Caribou Mountain study lakes.

Lake	W_o (ha)	A_o (ha)	Volume (10^3 m^3)	Z_m (m)	Slope (%)	Upland (%)	Peatland (%)	Disturbance (%)	τ (days)
Reference lakes									
C1	663.2	52.3	510	1.07	1.5	1	94	0	75
C2	614.8	93.4	1 910	2.17	2.3	2	95	0	217
C5	1068	76.5	568	0.75	2.4	6	79	0	80
C6	260.4	91.1	261	0.30	3.1	16	79	0	55
C7	569.0	90.0	578	0.66	2.9	6	87	0	61
C8	8208	60.8	612	0.99	1.4	5	85	0	49
C9	146.3	86.1	1 563	1.83	2.6	13	86	0	551
C11	204.8	134.4	4 071	3.06	6.1	65	35	0	887
C30	3218	536.1	55 564	11.60	2.0	28	67	0	770
C32	3018	953.4	27 318	2.90	3.0	12	81	0	314
C34	5571	166.5	5 840	3.50	4.0	22	77	0	194
C35W	825.0	175.0	18 240	5.50	6.1	32	66	0	419
C45	4627	1173	93 840	8.00	4.0	14	83	0	660
C47	2732	59.0	697	1.18	6.0	72	25	0	56
Lakes in catchments burnt in 1995									
C17	700.9	164.8	2 300	1.54	1.9	83	16	80	105
C23	1053	65.8	2 436	4.10	1.9	19	80	90	32
C24	1761	159.8	10 332	6.36	3.6	35	62	95	42
C25	820.1	151.9	4 278	2.87	4.2	25	72	90	171
C26	1520	36.6	523	1.68	3.3	25	73	75	36
C27	581.1	28.1	220	0.85	6.0	30	69	60	43
C41	32.6	2.6	22	0.86	2.0	43	57	100	68
C42	34.3	7.4	53	0.72	3.0	51	49	98	96
C43	691.9	8.3	50	0.60	4.0	51	45	95	26
C46	359.4	4.4	25	0.58	6.0	44	51	60	44
Lakes in catchments burnt between 1961 and 1985									
C12	642.9	40.5	440	1.22	2.9	6	88	20	101
C13	483.8	175.5	1 745	1.04	1.3	12	81	80	133
C14	268.9	62.4	1 779	2.93	4.3	27	73	80	298
C15	2257	128.3	2 013	1.67	2.8	6	91	70	77
C16	995.1	53.4	1 056	2.04	4.2	42	55	80	129

Note: W_o, watershed area; A_o, lake surface area; Z_m, lake mean depth; τ, residence time. Slope, upland, and peatland are percentages for each catchment and disturbance is the percentage impacted by forest fire.

al. 1992). Soluble reactive phosphorus (SRP) concentrations were measured by molybdate blue absorption from membrane filtrate within 24 h of collection. NH_4^+-N and NO_3^--N samples were frozen in 125-mL polyethylene bottles for analysis with indophenol blue (NH_4^+-N) and cadmium reduction (NO_3^--N) with automated colorimetry (Technicon methods 100-700 W/B and 155-71W). Total suspended solids, nonvolatile suspended solids (NVSS), and volatile suspended solids (VSS) were collected on preashed GF/F filters (mean particle retention 0.7 μm) and analyzed in duplicate after American Public Health Association (1993). Total and bicarbonate (HCO_3^-) alkalinities were estimated with the Hach phenolpthaline/bromocresol method (American Public Health Association 1993). Filtrate from GF/F filters for analysis of cations (Ca^{2+}, Mg^{2+}, Na^+, K^+), dissolved organic carbon (DOC), and anions (Cl^-, SO_4^{2-}) were stored in 60-mL polyethylene bottles. Cation samples were preserved with 60 μL of 40% H_2SO_4, while DOC and anion samples were refrigerated. Cations were analyzed by atomic absorption flame spectroscopy (Perkin-Elmer AS90 and AA3300), DOC by high-temperature catalysis (Shimadzu TOC-5000), and SO_4^{2-} and Cl^- concentrations by chromatography (Dionex 2000i/SP). Total suspended chlorophyll was collected on Gelman A/H filters (mean particle retention 1.2 μm) in duplicate from each of the three composite sample bottles. Filters were subsequently desiccated with silica-gel and frozen. Total chlorophyll *a* (CHL) was extracted with 90% ethanol (Sartory and Grobbelaar 1986) and concentrations were determined with fluorometric methods (Knowlton 1984).

Summer mean (June – early September) values are used in all analyses. Data are presented as box and whisker plots where the box outlines 25–75% of the data and whiskers denote 10–90% of the data. The line within each box represents the median value. pH values were converted to $[H^+]$ prior to averaging and analysis and converted back to pH for reporting. Data were tested for deviation from a normal distribution using Kolmogorov–Smirnov at $P = 0.05$. Data were either normally distributed or were $\log_{10}$ transformed to meet assumptions for normality and were analyzed with *t* test, Pearson's correlation, and univariate least-squares regression. Probability values and correlation coefficients are reported for these tests. We specify when nonnormal data were analyzed with nonparametric tests (Mann–Whitney *U*). ANCOVA was used to test differences in linear regressions between burnt and reference systems. We used discriminant analysis to determine if reference and burn-impacted lakes were different in measured catchment and lake physical characteristics. Percent open water could not be in-

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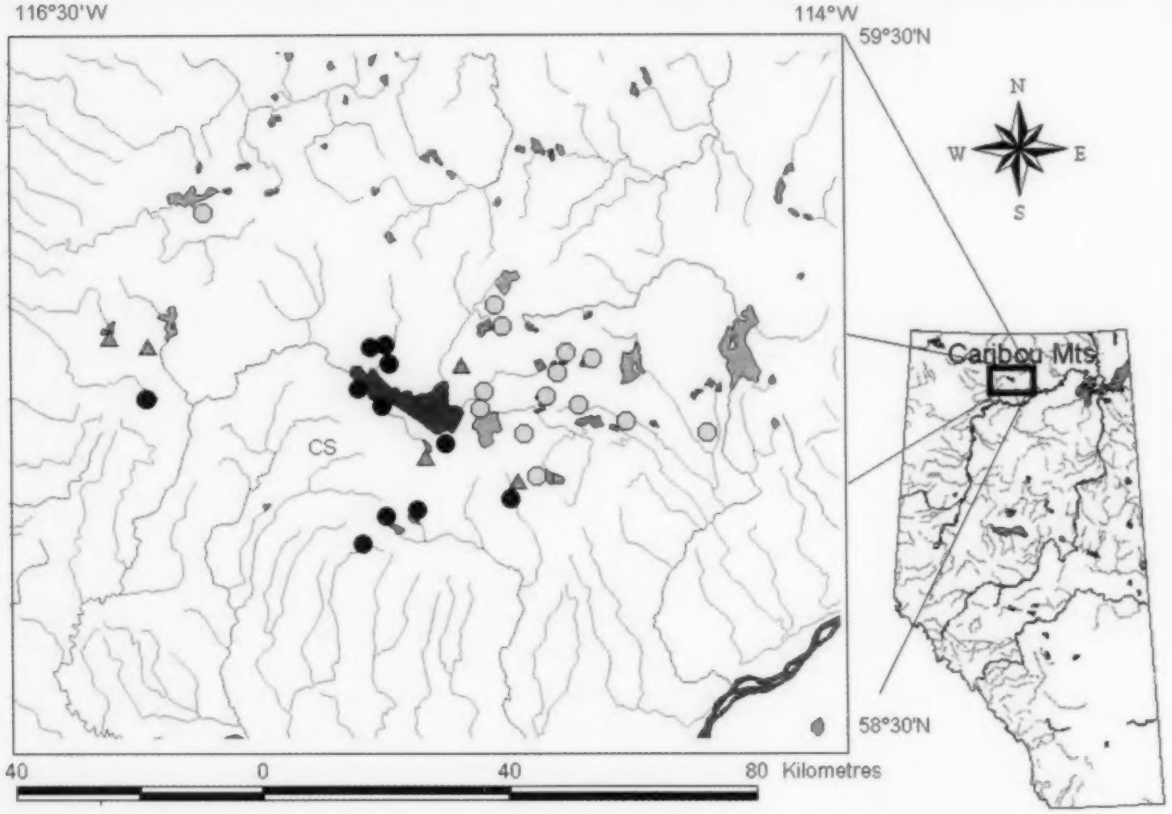
Fig. 1. Location of Caribou Mountain study lakes in Alberta, Canada. Reference sites (gray circles) contain lakes with no fire in their catchments since approximately 1910, previously burnt sites (triangles) contain lakes with catchments burnt between 1961 and 1985, and burnt sites (black circles) contain lakes in catchments burnt in 1995. An automated climate station (CS) operated for 2 years.



cluded in the discriminant analysis because of zero values. Differences were deemed significant at $P = 0.05$. All analyses used Statistica 4.1 and StatView 4.5 for Macintosh.

Results

Fire impacts on water chemistry

Several physical characteristics of lakes and their catchments differed between burnt and reference systems (Table 1). Reference lakes tended towards larger surface areas (Mann–Whitney, $P = 0.02$), lake volumes (Mann–Whitney, $P = 0.05$), and percent open water cover per catchment (Mann–Whitney, $P = 0.01$). Percent open water averaged 5 and 1% of reference and burnt catchments, respectively. The small proportion of open water and its concentration in collapse scars, areas of degraded permafrost, make it unlikely that it contributed to chemical differences in the lakes. Drainage ratios (watershed area (W_o)/lake surface area (A_o)) and A_o to volume (V) ratios, considered more important in determining land–water linkage than W_o or A_o alone, were not different between burn-impacted and reference lakes ($P = 0.6$ and 0.3, respectively). Slope was also not different between burn-impacted and reference catchments ($P = 0.3$). Discriminant function analysis, containing drainage ratio, A_o/V, catchment slope, and percent upland contained one root and was not significant (Wilk's $\lambda = 0.75$, canonical $r = 0.5$, $P = 0.3$). Likewise, substituting A_o, W_o, and V for W_o/V and W_o/A_o did not produce a significant discriminant function ($P = 0.2$). Therefore, it is unlikely that chemical differences observed between reference and burn-impacted lakes resulted from physical characteristics alone.

Total base cation concentrations (Ca^{2+}, Mg^{2+}, Na^+, K^+) of Caribou Mountain lake water (median 0.52 mequiv.·L^{-1}) were all below the world average for freshwater (2.33 mequiv.·L^{-1}). There were no detectable differences in mean total base cation concentrations (Fig. 2) between burnt (0.61 mequiv.·L^{-1}) and reference (0.72 mequiv.·L^{-1}) lakes ($P = 0.53$). As a percentage of total cations, Ca^{2+} was lower and K^+ was higher in burnt compared with reference lakes ($P < 0.05$).

Fire affected lake acidity and ion balances, possibly through increases in organic anions in burnt lakes. Lake water in burnt catchments was moderately acidic relative to reference lake water (mean pH = 6.9 and 7.6, respectively, $P = 0.04$). Burnt lakes demonstrated low total alkalinity compared with reference lakes; however, differences in means were not detectable (16.7 and 30.3 mg $CaCO_3$·L^{-1}, $P = 0.07$) (Fig. 2). Sulfate concentrations were elevated in burnt lakes (Mann–Whitney, $P = 0.01$) compared with reference lakes,

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Fig. 2. Summer mean total base cations, total alkalinity, and pH for lake waters in reference (open boxes, n = 14) and burnt catchments (shaded boxes, n = 10). Letters above the boxes indicate differences between reference and burn-impacted lakes ($P < 0.05$).

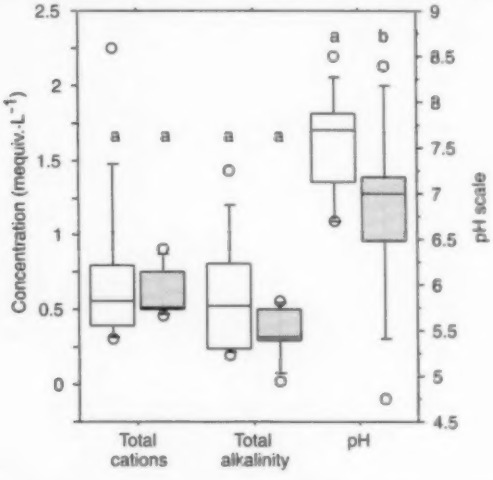
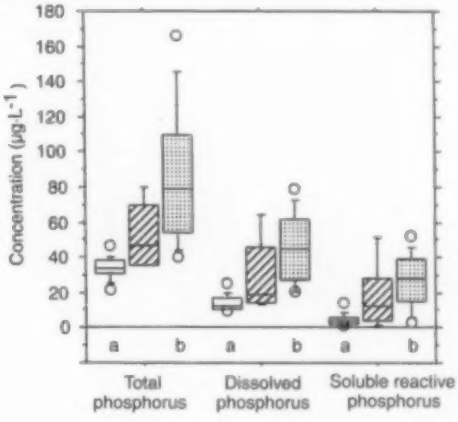


Fig. 3. Summer mean concentrations of TP, DP, and SRP for reference (open boxes, n = 14), burnt (shaded boxes, n = 10) and previously burn-impacted lakes (hatched boxes, n = 5). Letters above the boxes indicate differences between reference and burnt means ($P < 0.05$). Analytical statistics were not applied to previously burnt lakes.

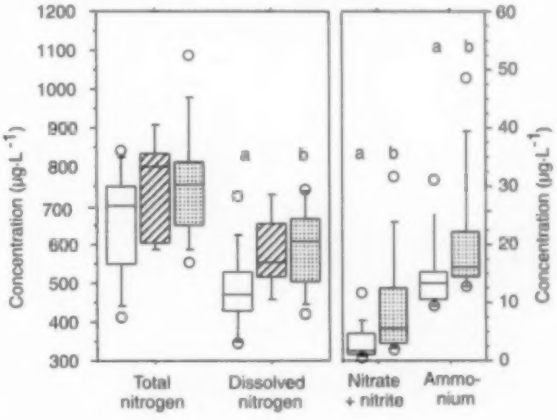


with median concentrations of 2.4 and 1.5 mg·L^{-1}, respectively. Fire did not affect chloride concentrations, which averaged 0.15 and 0.13 mg·L^{-1} for burnt and reference lake water, respectively (P = 0.3). Mean total anions (SO_4^{2-}, Cl^-, HCO_3^-, NO_3^-) balanced mean total cations in reference lake water (mean = 0.723 mequiv.·L^{-1}, P = 1.0). All lakes in burnt catchments had a deficit in total anions (0.46 mequiv.·L^{-1}, $P << 0.01$). The average deficit of 25% below mean total base cations suggested a large pool of organic acids in burnt lakes. Most *Sphagnum*-derived acids contain –COOH groups, which act as anions in solution while contributing protons (Clymo 1984). Anion deficits were linearly correlated with DOC in burnt (r^2 = 0.84, $P << 0.01$, n = 10) and less so in reference lakes (r^2 = 0.26, P = 0.06, n = 14). Fire apparently increased organic anion concentrations along a relationship with DOC that also existed in reference lakes.

Lake water in burnt catchments had elevated phosphorus and nitrogen concentrations. In reference lakes, mean TP, DP, and SRP concentrations were 33, 14, and 4 µg·L^{-1}, respectively (Fig. 3). Lake water in burnt catchments had 2.6-, 3.2-, and 6.8-fold higher TP, DP, and SRP concentrations, respectively, than reference lakes ($P << 0.01$). In reference lakes, mean TN, DN, NO_3^--N, and NH_4^+-N were 655, 488, 3, and 15 µg·L^{-1}, respectively (Fig. 4). Burn-impacted lake water contained 1.2-fold higher DN (P = 0.02), threefold higher NO_3^--N (P = 0.04), and 1.4-fold higher NO_3^--N (Mann–Whitney, P = 0.03) concentrations. Mean TP and DP in the two reference streams (MS1 and MS2) were 48 and 28 µg·L^{-1}, while the burn-impacted stream (MS3) contained 5.4-fold higher TP and half the DP. Mean TN and DN concentrations for water in MS1 and MS2 were 710 and 650 µg·L^{-1}, respectively, while MS3 contained 2.2-fold higher TN and 1.2-fold higher DN concentrations. Increased export of phosphorus and nitrogen from burnt relative to reference watersheds was likely given the two- to four-fold higher catchment-weighted discharge from MS3.

Caribou Mountain water had high concentrations of DOC,

Fig. 4. Summer mean TN and DN for reference (open boxes, n = 14), burnt (shaded boxes, n = 10), and previously burn-impacted lakes (hatched boxes, n = 5). NO_3^--N and NH_4^+-N are for reference and burnt lakes only. Letters above the boxes indicate differences in mean concentrations between reference and burnt lakes (P = 0.05).



particularly in burnt systems (Table 2). Lake mean DOC concentration in burn-impacted lake water (25 mg·L^{-1}) was 1.6-fold higher ($P << 0.01$) than in reference lakes (16 mg·L^{-1}). Further, in the reference streams MS1 and MS2, DOC concentrations averaged 33 and 37 mg·L^{-1}, respectively. In MS3, which drains a burnt area, DOC averaged 28 mg·L^{-1}. The three sampled fens contained almost identical DOC concentrations (45, 45, and 48 mg·L^{-1}) despite receiving drainage from burnt and unburnt areas. MS3 exported three and two times more DOC per unit catchment area than MS2 and MS1, respectively, given the two- to four-fold higher weighted discharge from MS3.

Caribou Mountain water was highly coloured, especially

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Table 2. Summary of chemical characteristics for the Caribou Mountain study lakes.

Lake	CHL ($\mu g \cdot L^{-1}$)	TP ($\mu g \cdot L^{-1}$)	DP ($\mu g \cdot L^{-1}$)	SRP ($\mu g \cdot L^{-1}$)	TN ($\mu g \cdot L^{-1}$)	DN ($\mu g \cdot L^{-1}$)	NO_3^--N ($\mu g \cdot L^{-1}$)	NH_4^+-N ($\mu g \cdot L^{-1}$)	DOC ($mg \cdot L^{-1}$)	DIC ($mg \cdot L^{-1}$)	VSS ($mg \cdot L^{-1}$)
C1	9.87	31	16	6	609	514	2.6	17.8	22	6.3	1.35
C2	16.58	38	20	9	744	527	11.6	31.2	18	5.8	3.49
C5	12.17	34	11	6	688	452	1.1	10.1	17	5.4	3.21
C6	14.51	36	10	5	823	474	3.2	13.3	12	4.7	4.63
C7	24.94	46	17	2	756	470	1.4	10.6	17	4.3	4.64
C8	4.68	40	25	14	661	612	5.0	13.6	27	7.6	1.57
C9	9.42	32	13	3	729	528	4.6	9.3	12	7.6	4.28
C11	6.79	31	11	2	750	585	1.2	15.4	12	14.8	1.73
C30	4.74	22	9	3	412	349	7.0	14.4	13	8.3	0.80
C32	7.73	32	12	2	445	345	1.0	10.9	11	3.5	2.20
C34	6.66	26	13	1	550	466	1.7	11.5	18	11.5	1.40
C35W	22.72	38	12	4	710	429	0.6	25.2	16	11.2	3.60
C45	9.22	26	11	1	454	361	4.9	12.2	10	7.7	1.80
C47	12.59	35	17	5	840	723	1.1	13.5	27	10.6	1.76
C17	39.23	125	66	36	1086	561	31.8	48.6	18	6.7	5.92
C23	5.94	79	55	40	552	468	6.1	12.9	22	6.3	1.70
C24	10.67	78	62	40	622	505	16.3	18.7	19	6.4	1.71
C25	24.31	55	21	9	751	421	2.6	12.7	14	6.2	4.16
C26	5.15	109	47	32	718	636	5.7	14.4	30	7.6	1.46
C27	3.89	98	43	24	649	583	12.6	16.1	27	8.4	1.12
C41	11.77	48	28	15	871	741	3.0	16.1	32	9.6	1.78
C42	5.97	40	21	4	757	668	5.6	22.2	21	14.6	1.59
C43	20.05	166	79	52	811	664	1.9	30.0	31	7.1	5.51
C46	7.26	54	33	17	779	734	4.2	15.5	35	8.9	2.02
C12	11.59	36	19	12	809	630	20.3	18.3	23	6.8	2.76
C13	19.74	46	14	2	799	534	3.8	70.9	14	6.5	4.27
C14	9.03	36	15	5	588	456	11.4	91.7	12	12.0	1.42
C15	4.89	80	64	51	607	556	9.0	19.9	27	6.3	1.09
C16	14.29	67	40	21	907	728	42.4	76.2	27	5.4	2.85

Note: Values are summer means. TC – TA is total cations minus total anions.

within burnt catchments. Reference lake water mean colour was 151 mg $Pt \cdot L^{-1}$ and ranged from 26 to 388 mg $Pt \cdot L^{-1}$, comparable with lake water colour in the boreal mixedwood ecoregion to the south, where colour ranged from 8 to 358 mg $Pt \cdot L^{-1}$ (E.E. Prepas, unpublished data). Mean colour in burn-impacted lake waters (342 mg $Pt \cdot L^{-1}$) was 2.3-fold higher ($P << 0.01$) than in reference lakes. Colour was related to DOC in all lake waters (Table 3). Variance in light penetration was closely associated with colour of lake water; the natural logarithm of Secchi transparencies was negatively related to colour, while light extinction coefficients were positively related to colour (Table 3). Mean Secchi transparencies in burn-impacted lakes (0.73 m) were 54% of those in reference lakes ($P << 0.01$), while the mean light extinction coefficient ($0.787 \cdot m^{-1}$) was 1.7-fold higher in burn-impacted lakes ($P << 0.01$) compared with reference lakes. Secchi depth and light extinction were correlated ($r^2 = 0.36$, $P < 0.01$, $n = 24$); when lakes C24 and C45 were removed, the relationship was stronger ($r^2 = 0.85$, $P << 0.01$, $n = 22$). Lake C24 had a high extinction coefficient ($1.28 \cdot m^{-1}$) for its Secchi depth (1.0 m) due to the continuous surface bloom of *Aphanizomenon* sp. as flakes. Lake C45 had a high extinction ($0.54 \cdot m^{-1}$) for its Secchi depth (2.8 m) due to wind conditions during sampling. Elevated DOC and colour in burn-impacted lakes reduced transparency and likely enhanced the potential for light limitation of phytoplankton growth after fire.

Fire affected inorganic suspended solids concentrations. Mean NVSS in reference lakes was 0.65 $mg \cdot L^{-1}$, whereas burnt lakes contained twofold higher NVSS (Mann–Whitney, $P = 0.04$). VSS concentrations were not different between reference and burnt lakes, averaging 2.6 and 2.7 $mg \cdot L^{-1}$, respectively ($P = 0.88$). Increased transport of inorganic particles from burnt catchments is inferred.

Fire did not appear to affect lake water CHL concentrations. Among reference lakes, mean CHL was 12 $\mu g \cdot L^{-1}$ and $\log_{10}$-transformed values were strongly related to TP ($r^2 = 0.83$, $P < < 0.01$, $n = 13$) (Fig. 5). Despite the much higher phosphorus concentrations observed in burn-impacted lake waters, CHL was not elevated, averaging 13 $\mu g \cdot L^{-1}$. There was no detectable relationship between CHL and TP concentrations for burn-impacted lakes ($r^2 = 0.06$, $P = 0.5$). We predicted CHL concentrations for burn-impacted lakes with the CHL–TP model for reference lakes. The residuals between predicted and observed values were positively related to Secchi depth ($r^2 = 0.44$, $P < 0.01$, $n = 10$) and to the TN:TP ratio ($r^2 = 0.69$, $P << 0.01$, $n = 10$). The lack of response in CHL to elevated phosphorus in burn-impacted lake

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NVSS ($mg \cdot L^{-1}$)	Ca^{2+} ($mg \cdot L^{-1}$)	Mg^{2+} ($mg \cdot L^{-1}$)	Na^{+} ($mg \cdot L^{-1}$)	K^{+} ($mg \cdot L^{-1}$)	SO_4^{2-} ($mg \cdot L^{-1}$)	Alkalinity (mg $CaCO_3 \cdot L^{-1}$)	Colour (mg $Pt \cdot L^{-1}$)	TC – TA (mequiv.$\cdot L^{-1}$)	pH
0.34	4.40	1.20	0.83	0.08	1.35	9.75	317	–0.1307	6.70
0.37	5.24	1.33	0.28	0.25	1.13	15.00	209	–0.0623	7.70
0.42	4.37	0.95	0.32	0.17	0.70	12.25	172	–0.0505	7.29
0.43	5.65	1.18	0.42	0.31	0.95	19.75	76	0.0128	7.86
1.13	4.12	0.94	0.41	0.22	0.82	11.25	205	–0.0601	7.08
0.91	7.30	1.59	0.37	0.09	1.55	15.25	389	–0.1755	6.69
0.83	8.06	1.91	0.54	0.43	1.05	32.50	34	0.0823	7.88
0.36	18.89	4.17	2.00	0.52	7.69	71.75	26	0.2147	8.49
1.00	10.40	2.00	0.60	0.40	2.30	36.75	105	0.0687	7.47
0.40	6.00	1.40	0.40	0.30	2.10	10.88	77	–0.1759	7.00
1.00	14.60	2.90	0.90	0.40	2.50	54.38	140	0.1287	7.82
0.90	11.00	2.40	0.90	0.50	4.20	40.50	112	0.1053	8.27
0.60	8.50	2.30	0.50	0.30	1.40	35.25	55	0.0965	7.77
0.41	27.01	7.67	6.01	0.49	48.73	59.00	196	–0.0542	7.68
1.84	6.46	1.62	0.85	0.62	2.71	16.50	240	–0.1192	8.38
2.28	7.18	1.35	0.47	0.57	1.63	16.25	331	–0.1395	7.06
0.84	6.04	1.36	0.57	0.82	2.66	15.50	250	–0.0886	6.94
1.09	7.84	2.27	0.53	0.79	2.70	27.75	112	–0.0052	7.96
1.02	12.07	3.06	0.82	0.50	7.04	25.25	480	–0.2479	7.10
2.87	10.24	2.38	0.91	0.34	1.96	26.50	396	–0.1819	7.17
0.51	5.37	1.78	0.69	1.11	9.51	1.13	424	–0.2474	4.75
0.30	5.98	1.85	0.74	0.70	5.43	16.00	212	–0.0638	6.61
1.51	6.54	1.59	1.20	0.61	7.96	6.75	456	–0.2174	6.06
0.82	10.20	2.68	2.76	0.24	16.62	15.00	523	–0.2079	6.48
0.65	7.35	1.58	0.63	0.05	1.23	16.25	312	–0.1728	7.20
0.62	6.71	1.94	1.30	0.25	1.54	26.50	112	0.0070	7.55
0.64	14.28	3.76	1.26	0.63	5.12	54.75	87	0.1132	7.93
0.81	5.67	1.47	0.81	0.33	3.49	10.00	454	–0.1741	6.60
0.89	7.91	1.98	0.51	0.29	5.34	12.75	344	–0.2161	7.26

Table 3. Univariate regressions for independent (X) and dependant (Y) variables.

X	Y	n	Intercept	Slope	r^2	SE of slope	MS error	F	P
DOC ($mg \cdot L^{-1}$)	Colour (mg $Pt \cdot L^{-1}$)	24	–156	19.3	0.89	1.44	2 595	175	<0.0001
Colour	ln Secchi (m)	24	0.62	–0.003	0.72	0.0004	0.066	53.6	<0.0001
Colour	ε (m^{-1})	24	0.32	0.001	0.58	0.0002	0.026	30.9	<0.0001
$\log_{10} W_o/A_o$	DOC ($mg \cdot L^{-1}$)	24	8.7	10.7	0.62	1.78	21.4	36.3	<0.0001
Burnt		10	10.1	12.2	0.69	2.87	17.2	17.9	0.003
Reference		14	9.04	8.0	0.68	1.60	10.8	25.1	0.0003
$\log_{10} W_o/A_o$	Colour (mg $Pt \cdot L^{-1}$)	24	9.17	210	0.57	38.9	10 205	29.2	<0.0001
Burnt		10	41.0	248	0.78	45.9	4 377	29.3	0.0006
Reference		14	18.4	141	0.59	34.8	5 131	16.4	0.0016
DI	$\log_{10}$TP ($mg \cdot L^{-1}$)	15	1.52	0.005	0.74	0.001	0.038	40.58	<0.0001
DI	$\log_{10}$DP ($mg \cdot L^{-1}$)	15	1.13	0.007	0.76	0.001	0.059	43.74	<0.0001

Note: ε, light extinction coefficient; W_o/A_o, drainage ratio.

waters and the relationship with Secchi depth are consistent with light limitation.

General patterns relating lake chemistry to catchment features were poor. There were no detectable relationships between nitrogen or phosphorus concentrations of lake waters with drainage ratio ($r^2 < 0.25$, $P > 0.3$). However, colour and DOC were linearly related to log drainage ratio (Table 3). Colour and DOC tended to increase at a faster rate with drainage ratio in burnt lakes compared with reference lakes (Table 3); however, the slopes of these relationships were not distinguishable (ANCOVA, $P = 0.09$ and 0.20, respectively).

Percent disturbance and time since disturbance

Water in the previously (1961–1985) burnt lakes had phosphorus concentrations intermediate between those of recently (1995) and nonburnt lakes. TP and DP concentrations for burnt lakes increased in a positive-linear relationship with percent disturbance (intercept forced through mean TP

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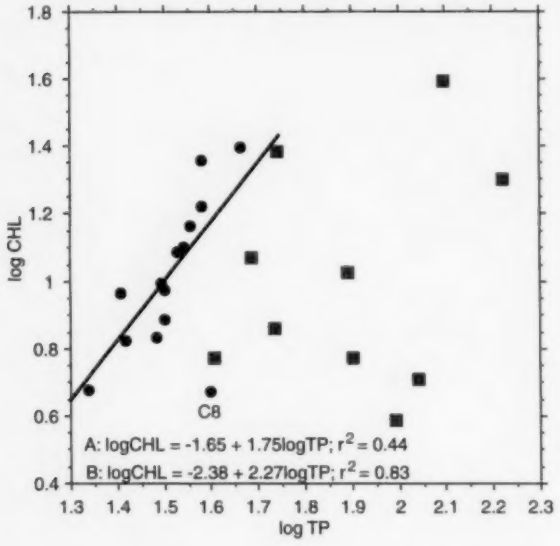
Fig. 5. Relationship between CHL and TP (both $\mu g \cdot L^{-1}$) for lakes in reference (circles) and burnt catchments (squares). Values are $\log_{10}$ transformed. A: equation and line for all reference lakes only; B: equation without C8, which deviates from other reference lakes because of its high colour (388 mg $Pt \cdot L^{-1}$).



and DP for reference lakes). TP and DP appeared to decline with the natural logarithm of time since disturbance. Data were not normally distributed in time or percent disturbance, so we combined both hypothesized disturbance patterns into a single disturbance index (DI):

$$DI = \% \text{ disturbance} \times e^{-Kt}$$

where t was time since disturbance (90 years for reference lakes) and K was a decay constant. The value for K was predicted from an exponential decay function $K = 0.693 \cdot T^{-1}$, where T was the half-life, which was estimated from the relationship between $\log_{10}$DP and TP and the natural logarithm of time since disturbance. The T was estimated at 11 and 20 years for DP and TP, respectively. The DI explained 74 and 76% ($P << 0.01$) of the variance in TP and DP, respectively, among the 15 impacted lakes (Table 3). We included reference conditions in the analysis by forcing the intercept through mean TP and DP concentrations for reference lakes (intercept value from Table 3) assuming that they represented a zero DI.

Discussion

Catchments in the Caribou Mountains are fundamentally different from those where fire effects have historically been studied. The large proportion of inundated peatlands in the Caribou Mountains created unique nutrient responses following fire. For example, forest fire usually augments NO_3^--N and, to a lesser degree, phosphorus export from granitic regions (Lewis 1974; McColl and Grigal 1975; Wright 1976). The relatively severe Caribou Mountains fire caused elevated phosphorus and, to a lesser degree, nitrogen concentrations in lakes, which suggested higher phosphorus compared with nitrogen export following fire. Similar findings are reported from other wetland systems. Burnt fens exported phosphorus and retained nitrogen, while burnt upland catchments exported nitrogen and held phosphorus in the granitic Experimental Lakes Area (Bayley et al. 1992). Nitrogen retention in Alberta peatlands typically exceeds 98% (Li and Vitt 1997), a value comparable with the greater than 85% retention reported by Bayley et al. (1992) for burnt fens. Surface water in northern Alberta, where peatlands dominate, could be more sensitive to eutrophication from elevated TP following fire than indicated by upland fire studies because of reduced phosphorus retention in peatlands after fire.

Increase in the flux of divalent cations and potassium from organic soils usually occurs after fire (Tiedemann et al. 1978). Increased flux rates of divalent ions from burned peat likely occurred in the Caribou Mountains. However, the cation exchange capacity of both living and dead peat likely remained intact, liberating protons as cations were exchanged (Clymo 1984). The result was a fivefold median increase in $[H^+]$, decreased pH, and reduced alkalinity in burnt lakes, while base cation concentrations did not change. Organic acids associated with elevated DOC in burn-impacted lakes possibly added to overall acidification while contributing organic anions (presumably $R–COO^-$).

The relationship between CHL and TP in reference lakes on the plateau indicates a strong association between phytoplankton biomass and TP. The slope for $\log_{10}$-transformed values (2.31) was more positive and the intercept (–2.46) more negative than values reported for North America (Nurnberg 1996).

A general model for the movement of water to lakes and streams in the discontinuous permafrost region of boreal Alberta may include groundwater systems or flow through organic peat. Surface runoff is minimal, even during intense storms, because the infiltration capacity of surface moss and peat (acrotelm) is about 1 $cm \cdot s^{-1}$, declining to 10^{-4} to 10^{-6} $cm \cdot s^{-1}$ in anaerobic peat (catotelm) layers (Ingram 1983). Groundwater could discharge through streambeds and lakes themselves, as they appear to be the only places without permafrost, other than the hydrologically disconnected collapse scars. Inputs from the peat layer should be restricted to a small effective contributing area when the water table is limited to the catotelm. Rain events that raise the water table to the acrotelm should cause a substantial increase in effective contributing area and loading of peat-derived water due to higher hydraulic conductivity in the acrotelm. Macropores, typically occurring at the peat–mineral interface (e.g., Hill 1993), may also be important in delivering water high in DOC and protons. However, water discharge from fens likely had a greater influence on surface water chemistry than that from bogs by virtue of their higher discharge rates (Halsey et al. 1997). Groundwater in the Caribou Mountains had base cation concentrations 20-fold higher than found in lakes (P. McEachern, unpublished data). The similarity between fen and lake water chemistry and the high cation concentrations of groundwater suggest that groundwater discharge to lakes was minimal and restricted to discharge through fens.

Time since disturbance and percent disturbance were important factors in nutrient enrichment among burnt lakes.

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When combined into a DI, they explained 74 and 76% of the variance in lake TP and DP concentrations, respectively. An exponential decay model for time since disturbance impacts was used because it matched the trend for our limited temporal data. The hypothesis is justifiable because recovery rates should initially be rapid as new growth and microbial communities are reestablished followed by a decrease with increasing time as microbial and plant communities stabilize and nutrients are flushed from the lake and lost to sediments.

Our results suggest that forest fire had a profound impact on surface water quality in the lakes of the Caribou Mountains. These lakes responded to fire with elevated nutrient concentrations because phosphorus and, to a lesser degree, nitrogen liberated during fire and subsequent decomposition were not retained by peat. Although base cations were likely liberated from burnt material, cation exchange with peat resulted in an increase in the flux of protons. Elevated phosphorus concentrations slowly returned to reference conditions depending on both the magnitude of disturbance (percent disturbance) and the time since disturbance. A single DI combining percent disturbance and time proved effective; however, a larger lake set spanning a range in time is needed to test the hypothesized exponential and linear components of this model. The effects of fire on water chemistry may be larger in peatland-dominated catchments than elsewhere, due to elevated export of phosphorus and long recovery periods.

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Effects of experimental clearcut logging on thermal stratification, dissolved oxygen, and lake trout (*Salvelinus namaycush*) habitat volume in three small boreal forest lakes

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Abstract: Clearcut logging around three 30- to 40-ha dimictic northwestern Ontario lakes was associated with increases of 5% or less in midlake wind speed and no measurable changes in spring and fall circulation efficiency or duration of stratification. Water clarity, indexed as the depth at which photosynthetically active radiation was 1% of surface intensity, declined by 25% after 3 years. Late-summer thermoclines were about 1 m shallower in two lakes after logging, but it was not possible to exclude weather as a factor. None of the lakes showed significant declines in lake trout (*Salvelinus namaycush*) habitat volume. A forested shoreline buffer strip around one of the lakes prevented increases in midlake wind speed but did not prevent declines in water clarity and thermocline depth.

Résumé : La coupe à blanc autour de trois lacs dimictiques de 30 à 40 ha du nord-ouest de l'Ontario a été associée à des augmentations de 5% ou moins de la vitesse du vent au milieu du lac, mais à aucun changement mesurable dans l'efficacité de la circulation printanière et automnale, ni dans la durée de la stratification. La limpidité de l'eau, calculée selon un indice de 1% de la profondeur du rayonnement photosynthétiquement actif, a baissé de 25% après 3 ans. Les thermoclines de la fin de l'été se trouvaient environ 1 m plus haut dans les deux lacs après la coupe, mais on ne pouvait pas exclure le rôle du facteur climatique. Dans aucun lac on n'a noté de baisse significative du volume d'habitat du touladi (*Salvelinus namaycush*). Une bande tampon boisée sur la berge autour d'un des lacs a empêché les augmentations de la vitesse du vent au milieu du lac, mais n'a pas empêché les baisses de la limpidité de l'eau ni le changement de la hauteur de la thermocline.

[Traduit par la Rédaction]

Introduction

For many years, Ontario lake managers have been concerned about the threat posed to lake trout (*Salvelinus namaycush*) populations by nutrient enrichment, sedimentation, and accelerated hypolimnetic oxygen depletion (HOD) following clearcut logging in the boreal forest (Ontario Ministry of Natural Resources 1988). This concern originated in part from studies in the 1960s and 1970s demonstrating the relationships between phosphorus and HOD in temperate lakes and evidence that logging and road construction had caused sedimentation and nutrient enrichment in streams in various parts of North America (e.g., Brown and Krygier 1971; Schindler et al. 1971; Cornett and Rigler 1979). Since then, various studies have reported water quality changes after logging around boreal lakes and streams (Holopainen et al. 1991; Rask et al. 1993, 1998; Carignan et al. 2000). In northwestern Ontario, new clearcuts, roads, and landings were associated with aeolian sediment transport into lakes (Steedman and France 2000) and minor littoral warming (Steedman et al. 1998). There is evidence that deforestation may increase wind exposure on very small lakes (Rask et al. 1993; Scully et al. 2000), but mixing in larger lakes is probably determined by topography, lake morphometry, and water colour (Fee et al. 1996).

Our understanding of lake trout habitat requirements is also evolving. New evidence suggests that lake trout are not fundamentally restricted to the hypolimnion of stratified lakes and that their realized thermal niche can be considerably broader than traditionally inferred from laboratory studies. This may be most apparent in small lakes with simple fish communities, as lake trout are now believed to forage extensively in epilimnetic water if other warmwater predators such as esocids or centrarchids are absent (Snucins and Gunn 1995; Sellers et al. 1998; Vander Zanden et al. 1999). Although our estimates of limiting temperatures for lake trout are being revised upwards, there is little doubt that lake trout are intolerant of dissolved oxygen concentrations below about 5–6 $mg \cdot L^{-1}$ (Sellers et al. 1998). Quantitative indices of lake trout habitat volume have traditionally been based on temperature and dissolved oxygen limits believed to impose significant restrictions on the behaviour or viability of lake trout individuals or populations. Two indices have been widely used by lake managers: (*i*) "optimal" habitat, the volume of water 10°C or colder, with dissolved oxygen of 6 $mg \cdot L^{-1}$ or higher (10/6 habitat), and (*ii*) "usable" habitat, the volume of water 15.5°C or colder, with dissolved

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oxygen of 4 mg·L^{-1} or higher (15.5/4 habitat) (MacLean et al. 1990; Evans et al. 1991; Ryan and Marshall 1994). Schindler et al. (1996) used 10°C and 4 mg dissolved oxygen·L^{-1} to define summer refugia for lake trout in the Experimental Lakes Area.

Five environmental factors have been strongly associated with the volume of lake trout habitat (i.e., cool, highly oxygenated water) in stratified temperate lakes (*i*) lake morphometry, relating primarily to effective fetch and total lake volume, (*ii*) thermocline depth, which determines the partitioning of lake volume into epilimnetic and hypolimnetic waters, (*iii*) HOD caused by decomposition of organic sediments, (*iv*) duration of stratification, the time that the hypolimnion is physically isolated from atmospheric oxygen, and (*v*) circulation efficiency, the amount of dissolved oxygen that is restored to deoxygenated hypolimnetic waters during fall and spring mixing (Molot et al. 1992; Ryan and Marshall 1994; Fee et al. 1996). Catchment deforestation could be expected to modify some or all of these factors through intermediate mechanisms involving decreased water clarity caused by increased loadings of dissolved organic carbon (DOC), nutrients, and sediment and by increased wind-induced mixing.

This study reports the effects of experimental catchment deforestation on wind exposure, water clarity, thermal stratification, and dissolved oxygen in three small northwestern Ontario lake trout lakes. The utility of various lake trout habitat indices was also examined. Water quality impacts are reported in a companion paper (Steedman 2000).

Methods

Study site

The three small headwater lakes monitored in this study (none are formally named) were located in the Ontario Ministry of Natural Resources' Coldwater Lakes Experimental Watersheds in boreal – Great Lakes transition forest on the Canadian shield, approximately 200 km northwest of Thunder Bay, Ontario, Canada (Table 1). The lake catchments had shallow soils with abundant boulders and bedrock outcrops, moderate slopes (15–50%), and relief generally not more than about 60 m. Catchment forests consisted of 75- to 100-year-old jack pine (*Pinus banksiana*), trembling aspen (*Populus tremuloides*), and black spruce (*Picea mariana*), with some paper birch (*Betula papyrifera*), eastern white cedar (*Thuja occidentalis*), red pine (*Pinus resinosa*), and eastern white pine (*Pinus strobus*). The lakes were relatively homogeneous with regard to solute and nutrient content, and extremely dilute, with specific conductance of about 14–22 μS·cm^{-1}, 2–3 mg DOC·L^{-1}, total phosphorus of less than 5 μg·L^{-1}, and chlorophyll *a* of less than 2 μg·L^{-1} (Steedman 2000). The lakes contain native populations of lake trout, white sucker (*Catostomus commersoni*), and five to seven species of smaller fish (primarily Cyprinidae, Gasterosteidae, and Etheostomidae).

Climate

Precipitation, wind speed, and wind direction were monitored at automated meteorological stations on a knoll in an upland clearcut, logged in 1987, 0.5 km northeast of L26 (beginning June 1993) and on rafts in the middle of L26, L39, and L42 200–500 m from shore (beginning May 1995). Before installation of the meteorological stations, rainfall was measured with manual rain gauges in the same locations. R.M. Young 05103 wind monitors were used at all stations, mounted 3 m above the ground at the upland site and 1.5 m above the water surface on the rafts. Data loggers sampled sensor readings at 5-s intervals and recorded hourly means and extremes. Because the climate monitoring network was not fully operational for the first few years of the 1991–1999 study period, surrogate thermal and precipitation indices were derived from available data to allow comparison of weather conditions throughout the study. These included average May–September L42 surface water temperature obtained from 1991–1999 water temperature profiles to provide an integrative index of air temperature during the open-water period and 1992–1999 June–September rainfall to provide an index of summer precipitation. The 1966–1988 climate normals for Atikokan, 70 km southeast of the study lakes, were obtained from Environment Canada.

Experimental clearcut logging

In 1996, after 5 years of predisturbance monitoring, the catchments of L26, L39, and L42 were partially deforested by commercial loggers using a tracked feller buncher and chainsaws. Trees were dragged by skidders to the nearest road and delimbed there (Table 2). L26 had a moderate amount of catchment deforestation (33%), with no disturbance of shoreline forest. L39 and L42 had extensive catchment (60–70%) and shoreline deforestation (40–60%). Some additional logging occurred on the shoreline of L42 and on intermittent stream catchments draining to L26 and L39 in 1998. Catchment and clearcut boundaries extended 100–600 m from the lakeshores. About 5 km of logging roads were constructed in the combined catchments of L39 and L42, and about 2 km of roads were constructed in the catchment of L26.

Limnology

Limnological data, including temperature–oxygen profiles, light profiles, and Secchi depth, were collected at weekly to bimonthly intervals (depending on season and location) at the deepest point of each lake. Most measurements reported here were from the open-water season, roughly mid-April through late October. The dates used for interannual comparisons were standardized for each type of measurement but varied between measurement types depending on the longest period of record that was represented in all study years.

Water temperature and dissolved oxygen profiles were measured with a YSI model 57 or model 58 meter at 1-m or smaller depth intervals. Complete spring or fall circulation was arbitrarily recognized when bottom waters achieved dissolved oxygen concentrations of at least 4 mg·L^{-1} after winter or summer anoxia. Dissolved oxygen levels near equilibrium with air (i.e., at least 8 mg·L^{-1} at 5–10°C) were recognized as evidence of complete and prolonged circulation. Since dissolved oxygen readings near lake bottom may be in error if the probe penetrates flocculent surficial sediments, these observations were based on the highest dissolved oxygen reading within 3 m of the estimated maximum lake depth. These data probably underestimate circulation frequency and extent, particularly for fall dates. Field crews were rarely on the lakes on the date of maximum fall mixing, which often occurred after boat operations were shut down for the winter. Late-fall mixing was inferred if measurements through the ice a month or two later indicated high dissolved oxygen levels near the lake bottom. Thermocline depth was calculated as the bottom of the measurement interval (usually 0.25–0.50 m in the metalimnion) with the highest temperature gradient. The lakes were considered to be thermally stratified when the maximum Brunt–Väisälä frequency N was 20·h^{-1} or more in a temperature–depth profile (MacIntyre and Melack 1995). This corresponded well in these lakes to a surface temperature of 10°C or more, which was used as a surrogate indicator of stratification, interpolated between measurement dates. Where surface water temperatures fluctuated above and below 10°C in the spring and fall, the earliest spring date and latest fall date were used to define strat-

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Table 1. Description of the study lakes and summary of experimental catchment disturbance.

	Lake		
	L26	L39	L42
Location	49°07′15″N, 92°08′45″W	49°05′30″N, 92°10′00″W	49°05′00″N, 92°09′30″W
Nominal experimental treatment	Moderate catchment deforestation, shoreline buffer	Extensive catchment and shoreline deforestation	Extensive catchment and shoreline deforestation
Terrestrial catchment area deforested (1996, 1996 + 1998), %	33, 45	62, 77	71, 74
Shoreline length deforested (1996, 1996 + 1998), %	0, 0	62, 62	42, 61
No. of tributary lakes	0	1 (L42)	0
Maximum depth (m)	37	23	18
Surface area (ha)	29	39	26
Lake volume (10^5 m^3)	40.8	46.4	21.5
Average depth	14.1	11.9	8.3
Maximum fetch (m) and orientation	900, N–S	1100, NE–SW	1100, N–S
Total catchment area (ha)	106	194	70
Ratio of terrestrial catchment area to lake surface area	2.6	1.9	1.6
Water renewal time (years)[a]	13.1	8.2	10.5
DOC ($mg \cdot L^{-1}$)[b]	2.1	2.2	2.5
Chlorophyll *a* ($\mu g \cdot L^{-1}$)[b]	1.4	1.7	1.8
Estimated size (average weight, g) of lake trout population[c]	428 (690)	265 (877)	273 (848)

[a]Based on 1995–1997 average local runoff of 0.293 $m \cdot year^{-1}$ (Beaty 1998).
[b]1991–1995 May–September average.
[c]Number of unmarked fish encountered during 1991–1998 fall netting of spawning aggregations on L26 and L42 and in spring netting during 1995–1998 on L39.

Table 2. Description and timing of experimental logging impacts around the study lakes in 1996 and 1998.

		Forestry treatment	
Lake	End of 1991 to 1996 preimpact period	1996: first logging impact[a]	1998: second logging impact
L26: moderate catchment deforestation, with shoreline buffer strip	Aug. 31, 1996	Sept. 1 to Oct. 31, 1996: moderate deforestation of catchment (33% of area) with no disturbance of shoreline forest within 30–90 m of lake; 9-ha stream subcatchment at south end of lake left unharvested	June 1–20, 1998: 9-ha stream subcatchment deforested (this deforested an additional 12% of lake catchment, for a total of 45%); no disturbance of shoreline forest
L39: extensive catchment and shoreline deforestation	July 7, 1996	July 8 to Aug. 15, 1996: extensive deforestation of lake catchment (62%) and shoreline (62%); 19-ha stream subcatchment at south end of lake left unharvested	June 1–15, 1998: 19-ha stream subcatchment deforested (this deforested an additional 16% of lake catchment, for a total of 77%); no additional disturbance of shoreline forest
L42: extensive catchment and shoreline deforestation	June 20, 1996	June 21 to July 31, 1996: extensive deforestation of catchment (71%) and shoreline (42%); temporary 30–40 × 500 m (about 1.8 ha) shoreline buffer strip left along southwest shore of L42	June 1–4, 1998: temporary shoreline buffer strip deforested (this deforested an additional 3% of lake catchment,[b] for a total of 74%, and an additional 19% of shoreline, for a total of 61%)

Note: Catchment areas refer to the terrestrial (i.e., nonlake surface) portions. Shoreline deforestation refers to the length of shoreline where merchantable trees were cut to the water's edge.
[a]The 1996 clearcuts were lightly scarified in July and August 1997, and slash piles were burned in October 1997. The 1998 clearcuts were not scarified.
[b]Deforestation of the temporary buffer strip on L42 also constituted a 1% additional disturbance of the 144-ha L39 catchment. This has been included in the 1998 L39 disturbance figure of 16%.

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ification. Detailed digital bathymetric maps (1-m depth resolution) were used to calculate lake strata volumes for lake trout habitat volume indices. In addition to 10/6 and 15.5/4 lake trout habitat (see Introduction), two indices with higher temperature limits were calculated for comparative purposes, based on the observations of Sellers et al. 1998: "20/6 habitat," the volume of water 20°C or colder, with dissolved oxygen of 6 $mg \cdot L^{-1}$ or higher, and "/6 habitat," the volume of water with dissolved oxygen of 6 $mg \cdot L^{-1}$ or higher, with no upper temperature limit. Lake bathymetry was corrected for lake stage on all open-water sampling dates, based on daily interpolation of weekly stage measurements. June lake stages for all lakes in all years were within 0.3 m of the bathymetric datum.

Water transparency was measured at 1-m depth intervals with an upward-facing LICOR cosine-corrected photosynthetically active radiation (PAR) sensor and a LI-1000 data logger. Simultaneous light measurements of ambient light were recorded from a similar sensor located on the boat deck. An epilimnetic light extinction coefficient was calculated as the average incremental light extinction from 1.5 to 6.5 m depth, measured at 1-m intervals. This extinction coefficient did not include light reflection from the water surface. Surface light readings were used to correct sequential submerged readings for minor changes in surface light intensity. An incremental extinction coefficient was not calculated if surface light intensity changed by more than 10% between measurements. The 1% PAR depth was estimated as the depth of the first submerged reading showing ≤1% of surface radiation.

Statistical analyses

This study did not replicate lake treatments and therefore did not estimate between-lake variance associated with forestry impacts, i.e., the responses of each lake to its forestry treatment were analyzed and interpreted independently of the other lakes. However, interannual variability estimates for each lake, before and after logging impacts, were provided by the multiyear study design. Although L39 and L42 might appear to represent replicates of the "extensive deforestation" treatment, L42 was tributary to L39, and the lakes were not hydrologically independent. Data from 1996 were generally excluded from pre- and post-logging comparisons because summer averages from that year often spanned the period of logging.

Continuous wind data were available for the May 12 to October 31 period from 1995 through 1999 (1995–1998 for L26). Wind data had a skewed distribution and were transformed as $\log(n + 1)$ prior to calculation of means and 95% sample confidence intervals. Conventional analysis of variance (ANOVA) of these autocorrelated hourly time series would have been inappropriate, as significance of interannual differences in wind velocity would be greatly exaggerated. Instead, time series intervention analysis was used to estimate shoreline logging impacts on midlake wind velocity. Midlake wind velocity time series spanning upland and shoreline logging activity around L39 and L42 in 1996 and 1998 were modeled with "seasonal" Box–Jenkins or autoregressive integrated moving average (ARIMA) (1,1,1) (0,1,1) 24 models (Box and Jenkins 1976; SPSS, Inc. 1993). These ARIMA models differenced the data (subtracted each observation from the previous one) at hourly and daily lags to stabilize the time series. The models then estimated coefficients for hourly autoregression-1 and moving-average-1 processes and daily moving-average-1 processes to remove remaining autocorrelation in the data. Then, the remaining variance was partitioned according to a binary "dummy" variable set to 0 before the midpoint of each year's logging impact and to 1 after. All ARIMA analyses reported here produced residuals with no significant autocorrelation, a key diagnostic criterion for statistically valid partitioning of variance in autocorrelated time series data. Wind velocity data were not transformed prior to the ARIMA analysis because untransformed data produced better residuals, with impact coefficients in original units of metres per second.

Repeated-measures analysis of variance (RM-ANOVA) was used to estimate treatment effects for lake phenomena that were measured several times each year, including water clarity indices and thermocline depth. These data did not show consistently asymmetrical distributions and were not transformed. Each year's set of weekly to monthly measures was treated as an independent observation for the purposes of this study. RM-ANOVA does not allow missing observations, and in two cases where data were not measured in the required week, data from the previous week were used. Regular ANOVA was used to estimate treatment effects for minimum annual lake trout habitat volume, based on one observation per year. Bonferroni adjustment was used for all post hoc comparisons.

Results

The 1991–1995 prelogging period included a relatively wide range of temperature and precipitation, due in part to the June 15, 1991, eruption of Mt. Pinatubo in the Philippines, which brought unusually cool, wet weather in 1992. In general, the prelogging period had above-normal precipitation. Postlogging precipitation was below normal in 1997 and 1998 but increased in 1999 (Table 3). High winds (i.e., >10 $m \cdot s^{-1}$) occurred in all open-water months, from all directions. The strongest winds tended to blow from the southeast and the southwest and were most frequent in the spring and fall. Wind direction, strength, and seasonal patterns were generally similar between years.

Midlake hourly average and hourly maximum wind velocity increased slightly after logging on the two lakes with extensive shoreline deforestation. However, average wind velocity and 95% confidence intervals varied by less than 15% before and after logging, with highest average velocities in 1997, rather than after maximum deforestation in 1998 (Table 4). Intervention analyses of the L39 and L42 wind velocity time series produced impact coefficients of –0.1 to –0.4 $m \cdot s^{-1}$, with 95% confidence intervals spanning zero, a strong indication that no significant in-year increases in midlake wind were associated with the logging events. Average wind velocity at the upland meteorological station declined about 0.1 $m \cdot s^{-1} \cdot year^{-1}$ from 1995 to 1999, probably due to forest regeneration on surrounding clearcuts. The ratios of midlake to upland average wind velocity (corrected for the upland decline as estimated by linear regression) had a pattern consistent with increased postlogging wind velocity on L39 and L42 (Fig. 1). However, these were small increases of about 5% relative to the upland site.

Lake circulation occurred in late April to mid-May and again in late October to early November. The probability and efficiency of complete circulation were inversely associated with lake depth (Table 5). L26 (37 m deep) circulated in the spring every year after logging compared with only two of six years before logging. It rarely circulated in the fall and did not do so at all after logging. Circulation in L26 never fully restored deep dissolved oxygen levels. Circulation frequency in L39 and L42 was similar before and after logging. L39 (23 m deep) achieved complete spring and fall circulation in all years except fall 1993, with prolonged circulation about half of the time. L42 (18 m deep) had complete, pro-

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Table 3. 1991–1999 climate indices.

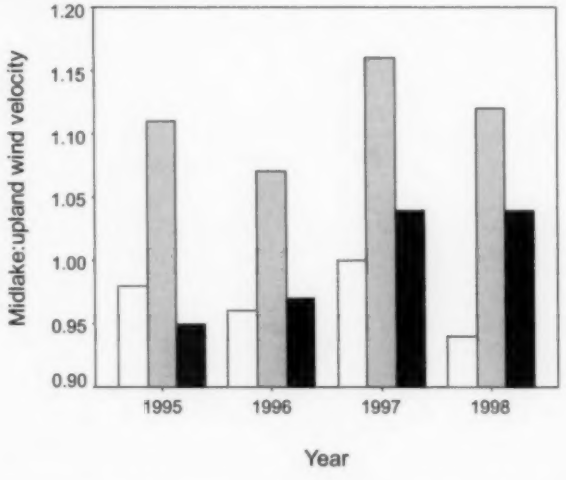
Climate index	Normal[a]	1991	1992	1993	1994	1995	1996	1997	1998	1999
L42 summer average temperature (°C)		20.8	16.2	16.7	18.3	18.7	19.6	17.5	19.3	17.9
March snowpack (mm equivalents)	182[b]				43		130	130	5	113
L42 approximate ice-off date		May 5	May 5	May 1	May 2	May 8	May 16	May 2	Apr. 15	Apr. 28
L42 approximate ice-on date		Nov. 5	Nov. 8	Nov. 15	Nov. 15	Nov. 2	Nov. 10	Nov. 12	Nov. 23	Dec. 1
Average stratification (days)		152	150	154	159	156	147	150	177	159
June–Sept. rainfall (mm)	393		483	414	489	434	440	277	257	409
Annual rainfall (mm)[c]	581				570	623	610	409	504	592

[a]1966–1988 Environment Canada Canadian climate normals at Atikokan, 70 km southeast of the study lakes (http://www.cmc.ec.gc.ca/climate/normals/ONTA006.HTM).
[b]Moisture content of total snowfall.
[c]1994–1999 data are April–October precipitation.

Table 4. 1995–1999 May 12 to October 31 midlake and upland mean and mean hourly maximum wind velocities ($m \cdot s^{-1}$, 95% sample confidence intervals in parentheses).

Lake	Year	Hourly mean	Hourly maximum mean
L26	1995	1.99 (0.38, 5.50)	4.26 (0.98, 12.97)
	1996	1.85 (0.34, 5.07)	4.09 (0.94, 12.40)
	1997	2.06 (0.38, 5.82)	4.46 (1.03, 13.69)
	1998	1.90 (0.32, 5.36)	4.21 (0.94, 12.95)
L39	1995	2.26 (0.48, 6.18)	4.61 (1.23, 13.09)
	1996	2.07 (0.36, 5.95)	4.38 (1.10, 12.80)
	1997	2.39 (0.51, 6.61)	4.85 (1.31, 13.80)
	1998	2.26 (0.50, 6.07)	4.68 (1.29, 13.12)
	1999	2.30 (0.47, 6.44)	4.73 (1.25, 13.59)
L42	1995	1.94 (0.34, 5.45)	4.24 (1.04, 12.44)
	1996	1.88 (0.34, 5.19)	4.17 (1.04, 12.08)
	1997	2.14 (0.47, 5.71)	4.60 (1.25, 12.90)
	1998	2.10 (0.43, 5.75)	4.47 (1.17, 12.76)
	1999	2.08 (0.29, 6.38)	4.43 (1.00, 13.74)
Upland	1995	2.04 (0.53, 5.07)	4.58 (1.71, 10.49)
	1996	1.84 (0.45, 4.55)	4.21 (1.27, 10.93)
	1997	1.87 (0.45, 4.70)	4.36 (1.29, 11.54)
	1998	1.73 (0.44, 4.17)	4.16 (1.26, 10.78)
	1999	1.61 (0.39, 3.89)	3.99 (1.17, 10.47)

Fig. 1. Ratios of midlake to upland average wind velocity for the study lakes L26 (open bars), L39 (gray bars), and L42 (black bars), 1995–1998. Data are May 12 to October 31 annual averages. The 1996–1999 upland wind data were corrected for declines of 0.097 $m \cdot s^{-1} \cdot year^{-1}$ associated with forest regeneration around the upland climate station.



longed circulation in all years except spring 1995, 1995, and 1999.

Stratification duration averaged 156 days (all lakes and all years), spanning April 25 to October 24, and varied from 150 days in 1992 and 1997 to 177 days in 1998 (Table 3). The lakes were stratified an average of 8 days longer in the years after logging, due mainly to relatively warm April temperatures and early ice-off dates in those years. There was no indication that stratification on L39 and L42 was shortened relative to L26 after logging, as could be expected if wind energy increased after shoreline deforestation.

Summer average water clarity as indexed by 1% PAR depth had declined 3–5 m, or about 25%, by the third year after logging in all of the study lakes (Table 6). Measurements of Secchi depth and epilimnetic PAR extinction proved too variable to provide strong evidence of change, but this could also indicate that transparency declines occurred mainly in subepilimnetic waters. Although water clarity measurements varied considerably through the May–August monitoring period, early-summer and late-summer water clarity was generally similar.

Thermocline depths were most variable in early summer and tended to deepen over the summer from about 4 m in early May to about 9 m in late September. Three years after logging, June thermocline depths averaged 1–3 m deeper in all lakes, while September thermocline depths were about 1 m shallower in L26 and L39 but not in L42 (Table 7). However, the three study lakes had shown similar, synchronous changes in late-summer thermocline depths prior to deforestation (Fig. 2), particularly in 1996, which was

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Table 5. Occurrence of complete and complete, prolonged spring and fall circulation in the study lakes, 1991–1999, defined as restoration of at least 4.0 (x) or 8.0 (X) mg dissolved oxygen·L^{-1} within 3 m of maximum lake depth.

Lake	Season	1991	1992	1993	1994	1995	1996	1997	1998	1999
L26	Spring	x		x				x	x	x
	Fall		x			x				
L39	Spring	x	X	X	X	x	x	X	X	x
	Fall	x	X		X	X	X	x	X	x
L42	Spring	X	X	X	X	x	x	X	X	x
	Fall	X	X	X	X	X	X	X	X	X

excluded from the analyses in Table 7 because thermoclines that year were potentially influenced by both precut and postcut conditions. If 1996 is included as a "prelogging" year in Table 7, estimates of the 1999 declines in September thermocline depth shrink by about 0.2 m, and the 95% confidence intervals increase by about 40%.

All estimates of postlogging change in minimum lake trout habitat volume had 95% confidence intervals that spanned zero by a substantial margin (Table 8). L42 (which had about 20–25% of the lake trout habitat volume of L26 and L39, depending on the index) was the only lake that showed a consistent pattern of postlogging declines, with 15.5/4 habitat down about 40% in 1998 and 1999.

The indices showed different responses to seasonal changes in thermal stratification and HOD. The 10/6 and 15.5/4 habitat indices showed similar seasonal patterns, with low year-to-year variability and a strong downward trend during the thermally stratified period. The upper temperature limits of these two indices generally excluded epilimnetic water from June to September, and they therefore had upper boundaries somewhere in the thermocline from about 4 to 12 m depth. The 10/6 habitat was always in shorter supply than 15.5/4 habitat during the summer and always disappeared completely in L42 by September or October. The 15.5/4 habitat was never completely eliminated from L42, although it declined to around 10% of lake volume each September in L42 and to 20–40% in L39 and L26. High levels of 10/6 habitat were always restored during the month of October in all lakes. The 20/6 and /6 habitats were always relatively abundant in the study lakes. The 20/6 habitat volume was strongly affected when epilimnion temperature fluctuated above and below 20°C. This produced very high annual and interannual variability in the index during the thermally stratified period. L42 had the lowest amount of 20/6 habitat, with average annual minima of about 20–40% of lake volume. L39 and L26 had average annual minima of about 40–50%. The /6 habitat volume had low variability and was always greater than about 80% of lake volume in all three lakes. This index showed a slight downward trend during thermally stratified period, with annual minima in October.

Discussion

Although midlake wind speeds on the study lakes did not increase much after clearcut logging, average wind velocities close to lee shores probably increased to a greater extent. Shoreline forest should have an effect on wind velocity analogous to that of agricultural shelterbelts. In the lee of forested shelterbelts, wind velocity may be reduced by about 40–80% within five times tree height and by 20–60% between five and 10 times tree height, depending on forest type. On the windward side, velocity is reduced by 20–40% within one to two times tree height (Geiger 1965, cited in Bartholow 1989). A lee shore one day may be a windward shore the next, and on all but the smallest lakes, maximum nearshore wind exposure will be determined mainly by upwind fetch rather than local shoreline features. Where lakes are surrounded by steep terrain, trees are likely to be responsible for only a portion of the total shelter provided by shoreline features (Ying et al. 1994). In flat terrain, removing a shoreline windbreak of dense forest 20 m high would increase effective lake fetch by about 120 m, according to Geiger's (1965) data. Adding 120 m fetch to a lake with 1 km fetch could be expected to increase thermocline depth by about 0.2 m, according to the empirical relationship developed by Shuter et al. (1983). The study lakes showed an opposite effect, suggesting that the influence on thermocline depth of increased wind energy after logging was secondary to other factors such as reduced water clarity. Only small lakes in relatively flat terrain, with fetch less than a few hundred metres, should experience significantly increased wind exposure after shoreline deforestation. This has been shown for a 0.4-ha lake in Finland (Rask et al. 1993) and for a 4-ha lake basin in Michigan (Scully et al. 2000).

Our midlake wind measurements were consistent with data provided in Solinske (1982) but not with France (1997), who interpreted Solinske's (1982) data to suggest that easterly wind velocities on 56-ha Experimental Lakes Area L239 tripled after deforestation along the east shore of that lake. Our analysis of Solinske's (1982) entire July 7 to August 25, 1981, data set showed that easterly and westerly L239 midlake to upland wind speed ratios had broadly overlapping distributions, with means of about 0.89 and 0.81, respectively. Velocity of easterly midlake wind on L239 averaged about 2.2 $m \cdot s^{-1}$ (SD = 0.8 $m \cdot s^{-1}$), or about 0.6 $m \cdot s^{-1}$ lower than westerly winds during that monitoring period.

The development of relatively deep June thermoclines in all lakes and unusually efficient spring circulation in L26, in 1998 and 1999, were probably not associated with deforestation. Decreased water clarity measured in those years would be more likely to produce shallower thermoclines (Fee et al. 1996). There was no indication that L26, which retained all shoreline forest, experienced increased wind exposure as a result of upland logging. We speculate that deep spring thermoclines in L26 were associated with the warm and windy April and May weather that caused early ice melting in 1998 and 1999. Prolonged spring mixing was not in-

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Table 6. Water clarity indices in the study lakes before and after experimental logging, estimated by RM-ANOVA with years as cases and May–August monthly observations as repeated factors within years.

					Mean difference after logging			
Clarity index	Lake	*n* prelogging: years × months	*n* postlogging: years × months	Mean prelogging	1997–1999 pooled	1997	1998	1999
Secchi depth (m)	L26	5 × 4	3 × 4	8.1 (7.6, 8.7)	–0.3 (–1.0, 0.4)	–0.2 (–1.6, 1.2)	–0.0 (–1.4, 1.3)	–0.6 (–2.0, 0.7)
	L39	5 × 4	3 × 4	7.1 (6.2, 8.0)	–0.2 (–1.7, 1.1)	–0.5 (–2.7, 1.7)	0.7 (–1.5, 2.9)	–1.0 (–3.2, 1.2)
	L42	5 × 4	3 × 4	6.7 (5.9, 7.5)	–0.3 (–1.4, 0.7)	–0.8 (–2.8, 1.2)	0.1 (–1.9, 2.2)	–0.4 (–2.4, 1.7)
PAR extinction (m^{-1})	L26	2 × 4	3 × 4	0.22 (0.13, 0.30)	0.03 (–0.00, 0.07)	0.03 (–0.12, 0.17)	0.02 (–0.12, 0.17)	0.05 (–0.10, 0.19)
	L39	2 × 4	3 × 4	0.26 (0.13, 0.40)	0.02 (–0.11, 0.15)	0.01 (–0.22, 0.24)	–0.02 (–0.25, 0.20)	0.08 (–0.15, 0.30)
	L42	2 × 4	3 × 4	0.27 (0.25, 0.28)	–0.01 (–0.03, 0.02)	–0.02 (–0.04, 0.01)	–0.01 (–0.04, 0.02)	0.00 (–0.02, 0.03)
1% PAR depth (m)	L26	2 × 4	3 × 4	17.0 (16.7, 17.2)	–2.6 (–6.2, 0.9)	–1.5 (–1.9, –1.2)*	–2.0 (–2.4, –1.7)*	–4.3 (–4.7, –4.0)*
	L39	2 × 4	3 × 4	14.8 (10.4, 19.1)	–2.2 (–8.5, 4.1)	–1.1 (–8.7, 6.5)	–0.3 (–7.9, 7.2)	–5.2 (–12.8, 2.3)
	L42	2 × 4	3 × 4	13.4 (12.8, 14.1)	–0.9 (–4.7, 2.9)	0.1 (–1.0, 1.2)	–0.0 (–1.1, 1.1)	–2.7 (–3.8, –1.6)*

Note: Monthly observations were means of two to five weekly measurements. The prelogging period of record was 1991–1995 for Secchi depth and 1994–1995 for epilimnetic PAR extinction and 1% PAR depth. The 95% confidence limits are given in parentheses. Asterisks identify differences where the 95% confidence interval does not span zero.

Table 7. Thermocline depths (m) in the study lakes before and after experimental logging, estimated by RM-ANOVA with years as cases and weekly observations in June or September as repeated factors within years.

							Mean difference after logging		
Month	Lake	*n* prelogging: years × observations per year	*n* post-logging: years × observations per year	Calendar weeks used in analysis	Mean prelogging	1997–1999 pooled	1997	1998	1999
June	L26	6 × 4	3 × 4	23–26	4.6 (3.9, 5.3)	1.2 (–0.5, 2.9)	–0.4 (–2.3, 1.4)	2.1 (0.2, 3.9)*	1.3 (–0.5, 3.1)
	L39	6 × 4	3 × 4	23–26	4.7 (3.8, 5.6)	1.7 (–0.4, 3.7)	–0.3 (–2.7, 2.0)	2.1 (–0.2, 4.4)	3.2 (0.9, 5.6)*
	L42	6 × 4	3 × 4	23–26	4.5 (3.5, 5.4)	0.8 (–0.8, 2.4)	–0.3 (–2.9, 2.2)	1.5 (–1.1, 4.1)	1.4 (–1.2, 3.9)
Sept.	L26	5 × 3	3 × 3	36, 37, 39	9.3 (8.8, 9.8)	–0.2 (–1.4, 1.0)	0.6 (–0.6, 1.8)	0.2 (–1.0, 1.4)	–1.4 (–2.6, –0.2)*
	L39	5 × 3	3 × 3	36, 37, 39	9.3 (8.9, 9.7)	–0.2 (–1.1, 0.8)	–0.1 (–1.1, 1.0)	0.5 (–0.5, 1.6)	–1.0 (–2.0, 0.1)
	L42	5 × 3	3 × 3	36, 37, 39	9.5 (9.0, 10.0)	–0.1 (–0.5, 0.8)	0.4 (–0.8, 1.6)	0.2 (–1.0, 1.4)	–0.2 (–1.4, 1.0)

Note: Prelogging (1991–1995) annual cases were contrasted with postlogging (1997–1999) cases. The 1996 data were included as prelogging for June comparisons and excluded from September comparisons. The 95% confidence limits are given in parentheses. Asterisks identify differences where the 95% confidence interval does not span zero.

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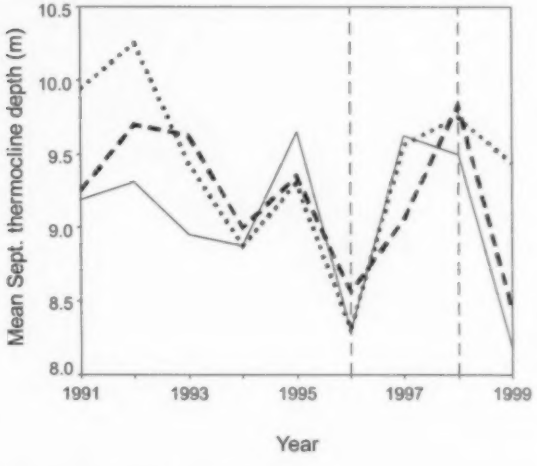
Table 8. Annual minimum values of various lake trout habitat indices (10^5 m^3) in the study lakes before (1991–1995) and after (1997–1999) logging, estimated by regular ANOVA.

			Mean difference after logging			
Lake	Index	Mean prelogging habitat volume	1997–1999 pooled	1997	1998	1999
L26	10/6	8.6 (7.0, 10.2)	0.7 (–2.6, 4.0)	–0.8 (–7.6, 6.0)	–0.9 (–7.7, 5.9)	3.8 (–3.0, 10.6)
	15.5/4	15.5 (13.8, 17.3)	0.5 (–1.7, 2.7)	0.7 (–6.9, 8.2)	–0.2 (–7.7, 7.3)	1.2 (–6.3, 8.7)
	20/6	20.6 (13.1, 28.0)	–2.6 (–11.5, 6.3)	–4.0 (–35.9, 28.0)	–2.1 (–34.1, 29.8)	–1.7 (–33.7, 30.2)
	/6	30.7 (28.6, 32.8)	0.9 (–2.1, 3.8)	1.6 (–7.3, 10.4)	–1.0 (–9.9, 7.9)	2.1 (–6.8, 10.9)
L39	10/6	3.2 (0.0, 6.0)	–0.3 (–4.1, 3.5)	0.9 (–11.0, 12.8)	–2.5 (–14.4, 9.5)	0.7 (–11.3, 12.6)
	15.5/4	12.6 (10.0, 15.2)	–0.9 (–4.7, 2.9)	–2.2 (–13.2, 8.8)	–2.1 (–13.1, 8.9)	1.7 (–9.3, 12.7)
	20/6	21.3 (9.4, 33.1)	–4.5 (–18.5, 9.6)	–3.5 (–54.2, 47.3)	–6.5 (–57.2, 44.3)	–3.5 (–54.3, 47.2)
	/6	36.9 (34.3, 39.5)	–4.0 (–9.1, 11.6)	–1.3 (–12.4, 9.7)	–2.0 (–13.1, 9.0)	–8.6 (–19.6, 2.5)
L42	10/6	0.0	0.0	0.0	0.0	0.0
	15.5/4	2.7 (2.0, 3.3)	–0.6 (–1.5, 2.1)	–0.3 (–3.1, 2.5)	–0.9 (–3.7, 1.9)	–0.8 (–3.6, 2.1)
	20/6	8.1 (1.5, 14.7)	–3.4 (–11.3, 4.5)	–2.0 (–30.2, 26.1)	–5.0 (–33.2, 23.1)	–3.2 (–31.4, 24.9)
	/6	17.3 (14.4, 20.3)	–1.6 (–6.1, 3.0)	–3.1 (–15.9, 9.7)	1.7 (–11.1, 14.5)	–3.3 (–16.1, 9.5)

Note: The 95% confidence limits are given in parentheses.

Fig. 2. Average September thermocline depths in the study lakes L26 (solid line), L39 (dashed line), and L42 (dotted line), 1991–1999. The vertical dashed lines show years when experimental logging occurred.



volved, since the delay between estimated ice-out and onset of stratification was about 9 days in 1998 and 4 days in 1999, somewhat shorter than the range of 8–15 days observed from 1994 to 1996.

Decreased September thermocline depths in all lakes in 1999 were consistent with postlogging DOC increases of up to 15%, chlorophyll increases of 15–30% (Steedman 2000), and concurrent measurements of decreased water clarity, particularly 1% PAR depth. Unlike thermocline depths, the declines in 1% PAR depth were unprecedented in the 1991–1996 prelogging record and were strongly suggestive of a logging impact. Deep phytoplankton communities that might cause subepilimnetic turbidity showed no significant changes from 1997 to 1999 in any of the study lakes (D. Graham, Department of Civil and Environmental Engineering, University of Kansas, Lawrence, KS 66045, U.S.A., unpublished data). However, decreased water clarity may have been associated with wet weather in 1999, which would have increased catchment exports of DOC and nutrients. Paleolimnological analyses of sediments from the study lakes have indicated that historical sediment accumulation and phytoplankton community composition were more strongly associated with long-term precipitation patterns than with episodic wildfire events in the lake catchments (Blais et al. 1998; Paterson et al. 1998).

Our observations of summer thermocline progression contrast somewhat with those of Schindler (1971) and Ryan and Marshall (1994), who suggested that thermocline depths in northwestern Ontario lakes were generally stable after onset of stratification. Thermocline progression of a metre per month complicates comparative studies where lake profiles are measured over an extended period (e.g., France 1997) and could account for some variation attributed to other factors such as wind exposure and water clarity.

The shoreline buffer strip around L26 probably influenced the response of that lake to clearcut logging by preventing the minor increases in midlake wind velocity that were observed on L39 and L42. However, the buffer strip did not prevent declines in water clarity and fall thermocline depth. These have the potential to increase lake trout habitat volume in the short term but did not appear to do so in this study, perhaps because the impacts were small. Such impacts would be compensatory to declines in habitat volume ultimately expected from increased lake productivity and HOD. Since none of the lakes showed changes in lake trout habitat volume as of 1999, the effectiveness of the shoreline buffer may be a moot point in that regard.

There are no reliable calibrations relating lake trout viability, productivity, age structure, or mortality to lake trout habitat volume indices. As a species, lake trout appear to tolerate a wide range of habitat conditions. Natural occurrence of lake trout in boreal lakes can be predicted reasonably well simply by the presence of thermal stratification, and viable lake trout populations can be found in lakes with habitat volumes far smaller than those proposed by Evans et al. (1991)

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as minimum safe values, particularly in lakes with simple fish communities (Marshall and Ryan 1987; Ryan and Marshall 1994; Sellers et al. 1998). However, indices of cool oxygenated water volume are useful for monitoring HOD in oligotrophic shield lakes subjected to catchment disturbance or nutrient inputs. Such indices will be most informative regarding threats to lake trout in lakes with complex epilimnetic fish communities, where lake trout are more likely to be restricted to the hypolimnion. Of the four indices examined, the 15.5/4 index appears to be the most useful general index of cool oxygenated water volume. During the period of thermal stratification, the 15.5/4 index showed a strong seasonal trend and low variability and was greater than zero (i.e., "stayed on the scale") in L42, the shallowest lake trout lake.

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Effects of experimental clearcut logging on water quality in three small boreal forest lake trout (*Salvelinus namaycush*) lakes

Robert J. Steedman

Abstract: Water quality was monitored in three 30-ha stratified headwater Precambrian Shield lakes for 5 years before and 3 years after moderate to extensive catchment deforestation. These lakes, which had water renewal times of about a decade, showed only minor changes in water quality by the third year after logging. Water quality response in a lake with moderate deforestation and intact shoreline forest was similar to that in two lakes with extensive upland and shoreline deforestation. By the second and third years after logging, May–September average volume-weighted concentrations of dissolved organic carbon, chlorophyll, total nitrogen, K^+, Cl^-, and Si had all increased, generally by about 10–40% over predisturbance levels, while Ca^{2+} and Mg^{2+} had declined by 10–25%. Dry weather the first year after logging was associated with temporary declines of 10–20% in dissolved organic carbon and chlorophyll.

Résumé : Nous avons surveillé la qualité de l'eau dans trois lacs de 30 ha de tête stratifiés du bouclier précambrien, pendant 5 ans avant et 3 ans après une déforestation modérée à généralisée des bassins versants. Ces lacs, dont la période de renouvellement était d'une décennie environ, ne présentaient que de faibles changements de la qualité de l'eau trois ans après la coupe. La réaction sur le plan de la qualité de l'eau dans un lac à bassin modérément déboisé et à rivage intact était la même que celle de deux lacs à bassin fortement déboisé sur les pentes et sur le rivage. Dès la deuxième et la troisième année après le déboisement, les concentrations moyennes de mai à septembre (après pondération pour le volume) du carbone organique dissous (COD), de la chlorophylle, de l'azote total, de K^+, de Cl^- et de Si avaient augmenté, généralement de 10 à 40% environ par rapport aux niveaux avant perturbation, tandis que le Ca^{2+} et le Mg^{2+} avaient baissé de 10 à 25%. La sécheresse qui a sévi la première année après le déboisement explique des baisses temporaires de 10 à 20% du COD et de la chlorophylle.

[Traduit par la Rédaction]

Introduction

Both wildfire and logging have been associated with elevated rates of carbon, cation, and nutrient (particularly nitrogen) export from boreal forest catchments, with the greatest impacts in the first or second year (Nicolson 1975; Bayley et al. 1992; Jewett et al. 1995). These impacts have generally been considered too minor to pose a significant threat to water quality in streams (Plamondon et al. 1982). Lake response to deforestation should resemble that of streams (Rask et al. 1993, 1998; Carignan et al. 2000) but may include delayed or reduced impacts related to dilution of runoff in lake volume. Although water quality is influenced by both wildfire and forest management, studies of recent sediments in northwestern Ontario lakes indicate that long-term precipitation patterns may have a greater effect on catchment erosion and lake productivity than either fire or clear-cutting (Blais et al. 1998; Paterson et al. 1998).

Lake trout (*Salvelinus namaycush*) lakes, with their clear, unproductive waters and cold-water biota, have been classified by resource managers as highly sensitive to logging impacts (Ontario Ministry of Natural Resources 1988). The purpose of this paper is to report a preliminary test of that assumption by quantifying water quality changes in three small lake trout lakes 3 years after experimental catchment deforestation by clearcut logging. Additional background and responses of water clarity, thermal stratification, and dissolved oxygen are reported in a companion paper (Steedman and Kushneriuk 2000).

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Methods

Study site

The three small headwater lakes monitored in this study (none are formally named) were located in the Ontario Ministry of Natural Resources' Coldwater Lakes Experimental Watersheds in boreal – Great Lakes transition forest on the Canadian Shield, approximately 200 km northwest of Thunder Bay, Ontario, Canada. The lake catchments had shallow sandy to organic soils with abundant boulders and granite outcrops, moderate slopes (15–50%), and relief generally not more than about 60 m. Catchment forests consisted of 75- to 100-year-old jack pine (*Pinus banksiana*), trembling aspen (*Populus tremuloides*), and black spruce (*Picea mariana*), with some paper birch (*Betula papyrifera*), eastern white cedar (*Thuja occidentalis*), red pine (*Pinus resinosa*), and eastern white pine (*Pinus strobus*). The lakes ranged in size from 26 to 39 ha, in maximum depth from 18 to 37 m, and had catchment to surface area ratios of 1.6–2.6 (Table 1). The lakes are stratified from May through October. Postlogging precipitation was about

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Table 1. Description of study lakes and summary of experimental catchment disturbance.

	Lake		
	L26	L39	L42
Location	49°07′15″N, 92°08′45″W	49°05′30″N, 92°10′00″W	49°05′00″N, 92°09′30″W
Nominal experimental treatment	Moderate catchment deforestation, shoreline buffer	Extensive catchment and shoreline deforestation	Extensive catchment and shoreline deforestation
% terrestrial catchment area deforested (1996, 1996 + 1998)	33, 45	62, 77	71, 74
% shoreline length deforested (1996, 1996 + 1998)	0, 0	62, 62	42, 61
No. of tributary lakes	0	1 (L42)	0
Maximum depth (m)	37	23	18
Surface area (ha)	29	39	26
Lake volume (10^5 m^3)	40.8	46.4	21.5
Total catchment area (ha)	106	194	70
Ratio of terrestrial catchment area to lake surface area	2.6	1.9	1.6
Water renewal (years)[a]	13.1	8.2	10.5

[a]Based on 1995–1997 average local runoff of 0.293 m·year^{-1} (Beaty 1998).

70% of normal in 1997 and 1998 and slightly above normal in 1999. Annual runoff constitutes about 10% of lake volume.

Experimental clearcut logging

In 1996, after 5 years of predisturbance monitoring, the catchments of L26, L39, and L42 were partially deforested by commercial loggers using a tracked feller buncher and chainsaws. Trees were dragged by skidders to the nearest road and delimbed there. L26 had a moderate amount of catchment deforestation (33% of area), with no disturbance of shoreline forest. L39 and L42 had extensive catchment (60–70%) and shoreline deforestation (40–60% of length). In 1998, some additional logging occurred on intermittent stream catchments draining to L26 and L39 and on the shoreline of L42, increasing catchment deforestation total to 45, 77, and 74%, respectively. Catchment and clearcut boundaries extended 100–600 m from the lakeshores. About 5 km of logging roads were constructed in the combined catchments of L39 and L42, and about 2 km of roads were constructed in the catchment of L26. A more detailed description of the experimental deforestation is provided in Steedman and Kushneriuk (2000).

Water quality

Water samples were collected at biweekly to monthly intervals, beginning in May 1991, in a plexiglass Kemmerer sampler at the deepest point of each lake. In 1991, sampling started at 1 m, with subsequent depths determined according to lake stratification. The 1992–1999 samples were collected at 5-m depth intervals starting at 0.5 m. Most samples were refrigerated and analyzed within 3–5 days. Some samples in 1996 and 1997 were frozen for several months prior to analysis. From 1991 to 1996, all water quality analyses were conducted by accredited laboratories of the Ontario Ministry of the Environment (MOE). Following provincial government downsizing in 1996, most analyses were shifted to LUCAS, a university-based laboratory in Thunder Bay. Most 1997–1999 water quality profiles included "top and bottom" split samples that were sent to MOE for quality control and calibration to pre-1996 methods. All LUCAS results reported here had linear relationships with monthly MOE split-sample results and were transformed according to batch-specific interlaboratory regression equations. If results from both laboratories were available for a water sample from a specific lake, date, and depth, MOE data were used. Chemical tests reporting "less than detection" were transformed to zero prior to numerical summary and analysis. Total phosphorus (TP) data quality was degraded after 1996, as LUCAS had a detection limit for TP of 5 $\mu g \cdot L^{-1}$, compared with 2 $\mu g \cdot L^{-1}$ at MOE. No other chemical tests had important interlaboratory differences in detection limits. Where occasional missing or less than detection results were encountered in depth profiles that had top and bottom MOE data and at least one valid result from an intermediate depth, neighboring values were used to estimate a result for that depth. Profiles requiring multiple estimates were removed from subsequent analyses. This occurred most frequently for TP from 1997 to 1999, for K^+ in 1995 and 1997, and for SO_4^{2-} in 1997. Specific conductance was measured with a temperature-compensated conductivity meter. Alkalinity and pH were measured simultaneously with an autotitrator. Dissolved organic carbon (DOC) was measured by infrared absorption after the sample was homogenized, acidified, and heated to 820°C in the presence of an O_2 carrier gas and platinum catalyst (MOE) or colorimetrically at 550 nm after acidification, purging with nitrogen, digestion by ultraviolet irradiation in the presence of persulfate, and diffusion of resulting CO_2 into a phenolphthalein indicator solution (LUCAS). Water samples for phytoplankton chlorophyll *a* (Chl *a*) were filtered (250 mL) through 1.2-μm-pore nylon membrane filters. The filters were wrapped in foil and frozen until analysis. Pigments were extracted into an acetone–water solvent and measured by spectrophotometry. Total Kjeldahl nitrogen (TKN) and TP were measured simultaneously by colorimetry after digestion with sulfuric acid in the presence of potassium sulfate and mercuric sulfate. Total nitrogen (TN) was estimated by summing TKN and NO_3^-. NO_3^- was measured by colorimetry after reduction with hydrazine (MOE) or by ion chromatography (LUCAS). Cations were measured by flame atomic absorption (MOE) or ion chromatography (LUCAS). Cl^- was measured by colorimetry after reaction with mercuric thiocyanate and ferric ion (MOE) or by ion chromatography (LUCAS). SO_4^{2-} was measured by ion chromatography. Silicate silica (Si) was measured colorimetrically by the molybdate method. Total suspended solids were measured gravimetrically. Metal concentrations were measured by ICAP after digestion in nitric acid and concentration by evaporation. Detailed digital bathymetric maps (1-m depth resolution) were used to calculate lake strata volumes centered vertically around each sampling depth. Whole-lake chemical mass estimates were calculated by summing parameter concentration (or 10^{-pH} in the case of H^+) times stratum volume for each depth stratum represented by a Kemmerer sample. Volume-

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weighted average concentration was calculated as whole-lake chemical mass divided by lake volume. Lake bathymetry was corrected for lake stage on all open-water sampling dates according to daily interpolation of weekly stage measurements.

Statistical analyses

This study did not replicate lake treatments and therefore did not estimate between-lake variance associated with forestry impacts, i.e., the responses of each lake to its forestry treatment were analyzed and interpreted independently of the other lakes. However, interannual variability estimates for each lake, before and after logging impacts, were provided by the multiyear study design. Although L39 and L42 might appear to represent replicates of the "extensive deforestation" treatment, L42 was tributary to L39, and the lakes were not hydrologically independent. Data from 1996 were excluded from pre- and post-logging comparisons because summer averages from that year spanned the period of logging for L39 and L42.

Prelogging water chemistry means and postlogging differences were estimated by repeated-measures analysis of variance (RM-ANOVA), with years as "independent" cases comprising May–September monthly water chemistry observations. Monthly observations were means of one to three measurements (generally at biweekly intervals) before 1996 and single monthly measurements after 1996. These data were neither highly nor consistently skewed and were not transformed prior to analysis. Bonferroni adjustment was used for all post hoc comparisons.

Results

The study lakes were all extremely dilute and unproductive, with average specific conductance of 14 (L42) to 22 μmho·cm^{-1} (L26) and Chl *a* less than 2 μg·L^{-1} (Table 2). Suspended solids and inorganic nitrogen were generally below detection in midlake surface waters. L26 had slightly higher alkalinity, pH, cations, and Si but lower TP, TN, and Chl *a* than L39 and L42. L42 generally had the lowest solute content (particularly Si, which was occasionally below detection) but had slightly higher DOC, TP, TN, and Chl *a* than the other lakes. Whole-lake volume-weighted average concentrations were closely representative of surface water conditions, due to the volumetric dominance of epilimnetic waters in these lakes. However, some substances showed depth gradients at various times of the year. During periods of thermal stratification, Chl *a*, TP, conductance, Si, SO_4^{2-}, and H^+ all increased with depth by amounts ranging from 10% to several hundred percent relative to the epilimnion, depending on date and dissolved oxygen conditions in the hypolimnion. DOC declined slightly with depth during summer stratification. Cations, TN, and alkalinity showed no vertical pattern during the summer. In late winter under ice cover, cations, Chl *a*, and DOC all showed declining concentrations with depth, possibly due to "freezing out" of solutes just below the ice.

The three study lakes showed similar patterns of postlogging water quality (Table 2). Dry weather the first year after logging (1997) was associated with temporary declines of 10–20% in DOC and Chl *a*. By 1999, DOC, Chl *a*, TN, K^+, Cl^-, and Si had increased by about 10–40% over prelogging averages. This was accompanied by a decline of 10–25% in the divalent cations Ca^{2+} and Mg^{2+}. The decline was most pronounced in L39 and L42, and in the case of Ca^{2+} continued through 1999. L26, which had the lowest level of catchment deforestation, showed the largest increases in TN, Na^+, and Si. DOC, TN, and Si appear to have peaked in the second year after logging in L26. There was no clear indication that maximum impact had occurred by the third year after logging in L39 and L42. Postlogging changes in conductance, alkalinity, pH, TP, and SO_4^{2-} were small relative to measurement uncertainty in all three lakes. Aluminum results were not available with sufficient frequency to include in the RM-ANOVA results. Average epilimnetic Al concentrations ranged from 9 (L42) to 13 μg·L^{-1} (L39) before logging and did not increase after logging.

Discussion

In the first 3 years after experimental logging, these lake trout lakes did not show much change in water quality. This was probably due to the fact that only a portion of each lake's volume was replaced by 3 years of postlogging runoff. Preliminary analyses show that runoff and export of nutrients, cations, and anions increased immediately after the 1998 experimental clearcuts on catchments of L26 and L39 tributaries (C. Allan, Department of Geography and Earth Sciences, University of North Carolina at Charlotte, personal communication). Even though total precipitation was below normal in 1997 and 1998, catchment export associated with the earlier and larger 1996 clearcuts probably increased in a similar way. The fall of 1996 was rainy, and spring runoff in 1997 was above average. Periods of below-normal runoff did not prevent significant changes in stream chemistry following wildfire at the Experimental Lakes Area (Bayley et al. 1992).

The limited water quality changes observed in the study lakes were indicative of slight nutrient enrichment of a magnitude unlikely to induce important changes in lake biota such as phytoplankton (Planas et al. 2000) or zooplankton (Patoine et al. 2000). Increased DOC in the lakes was probably responsible for a 25% reduction in water clarity and a 1-m decline in thermocline depth but was not associated with reductions in lake trout habitat (Steedman and Kushneriuk 2000). Continued monitoring is required to confirm and characterize long-term biotic impacts. These findings are generally consistent with the conclusion by Schindler et al. (1980) that catchment deforestation by wildfire was not likely to cause important water quality changes in Precambrian Shield lakes, unless water renewal time was short relative to the time required for catchment revegetation. Carignan et al. (2000) measured larger water quality changes in Quebec lakes with shorter water renewal times.

Forested shoreline buffer strips do not appear to strongly influence lake water quality response to catchment deforestation (Norris 1993). L26 water quality showed changes similar to those in the lakes with deforested shorelines, and Quebec lakes with catchments deforested to the shore by wildfire showed changes generally similar to those in logged lakes that retained 20-m-wide shoreline buffer strips (Carignan et al. 2000). On boreal forest lakes, shoreline buffer strips may be more important for preservation of aesthetic values and terrestrial habitat than for protection of water quality. This finding is significant, due to the extensive use of shoreline buffer strips designed to protect water quality and fish habitat during forestry operations. Existing fire

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Table 2. Whole-lake May–September volume-weighted water quality in L26, L39, and L42, prelogging (1991–1995) and postlogging (1997–1999).

Measure	Lake	Mean prelogging	Mean difference postlogging			
			1997–1999	1997	1998	1999
Conductance 25°C ($\mu mho \cdot cm^{-1}$)	L26	21.6 (20.7, 22.5)	–0.3 (–1.6, 1.0)	–0.8 (–9.1, 7.6)	–0.1 (–8.5, 8.2)	0.0 (–8.3, 8.4)
	L39	16.5 (15.2, 17.8)	0.9 (–1.0, 2.8)	–0.2 (–8.5, 8.1)	1.6 (–6.7, 9.9)	1.3 (–7.0, 9.6)
	L42	14.2 (12.8, 15.7)	0.9 (–1.2, 2.9)	–0.3 (–9.4, 8.9)	1.7 (–7.4, 10.9)	1.2 (–7.9, 10.4)
Alkalinity ($mg \cdot L^{-1}$ as $CaCO_3$)	L26	8.33 (7.91, 8.74)	–0.01 (–0.69, 0.69)	0.20 (–1.85, 2.25)	0.24 (–1.81, 2.30)	–0.41 (–2.47, 1.64)
	L39	5.93 (5.63, 6.23)	0.07 (–0.42, 0.56)	0.00 (–1.62, 1.62)	0.28 (–1.34, 1.90)	–0.08 (–1.70, 1.55)
	L42	4.92 (4.65, 5.19)	–0.25 (–0.69, 0.19)	–0.41 (–1.92, 1.10)	–0.12 (–1.63, 1.39)	–0.22 (–1.73, 1.29)
pH	L26	6.80 (6.66, 6.93)	0.14 (–0.11, 0.39)	0.03[a]	0.27 (–0.15, 0.68)	0.02 (–0.40, 0.44)
	L39	6.64 (6.52, 6.76)	0.17 (–0.05, 0.39)	0.09[a]	0.27 (–0.10, 0.65)	0.06 (–0.32, 0.44)
	L42	6.59 (6.46, 6.72)	0.14 (–0.11, 0.38)	0.07[a]	0.23 (–0.25, 0.71)	0.04 (–0.43, 0.52)
DOC ($mg \cdot L^{-1}$)	L26	2.1 (1.9, 2.3)	–0.1 (–0.5, 0.3)	–0.4 (–0.7, –0.2)*	0.3 (0.1, 0.5)*	–0.1 (–0.3, 0.2)
	L39	2.2 (2.0, 2.5)	0.1 (–0.3, 0.5)	–0.3 (–0.7, 0.0)*	0.3 (–0.1, 0.6)	0.3 (–0.1, 0.7)
	L42	2.5 (2.3, 2.7)	–0.1 (–0.5, 0.3)	–0.5 (–0.7, –0.3)*	0.1 (–0.1, 0.4)	0.1 (–0.2, 0.3)
Chl *a* ($\mu g \cdot L^{-1}$)	L26	1.39 (1.19, 1.59)	0.01 (–0.25, 0.37)	–0.05 (–1.21, –1.12)	0.01 (–1.16, 1.18)	0.21 (–0.95, 1.38)
	L39	1.73 (1.35, 2.11)	0.11 (–0.47, 0.70)	–0.15 (–1.77, 1.47)	–0.06 (–1.68, 1.56)	0.54 (–1.08, 2.16)
	L42	1.84 (1.57, 2.10)	0.09 (–0.31, 0.49)	–0.13 (–1.33, 1.07)	0.04 (–1.16, 1.24)	0.36 (–0.84, 1.55)
TP ($\mu g \cdot L^{-1}$)	L26	4 (3, 4)	–1 (–2, 0)	–2[b]	–1 (–3, 2)	–1 (–3, 2)
	L39	4 (3, 5)	0 (–1, 2)	–4[b]	1 (–2, 4)	0 (–3, 3)
	L42	6 (5, 6)	2 (0, 3)	–2[b]	2 (0, 5)	1 (–1, 4)
TN ($\mu g \cdot L^{-1}$)	L26	172 (163, 181)	42 (25, 57)*	28[a]	47 (9, 84)*	38 (1, 75)*
	L39	182 (171, 193)	37 (17, 58)*	–32[a]	33 (–12, 77)	42 (–29, 86)
	L42	247 (236, 258)	13 (–8, 33)	–77[a]	8 (–36, 52)	17 (–27, 61)
K^+ ($mg \cdot L^{-1}$)	L26	0.29 (0.26, 0.32)	0.04 (–0.02, 0.10)		0.03 (–0.10, 0.15)	0.06 (–0.07, 0.18)
	L39	0.24 (0.22, 0.25)	0.08 (0.05, 0.10)*		0.08 (0.01, 0.14)*	0.08 (0.01, 0.14)*
	L42	0.26 (0.22, 0.29)	0.04 (–0.03, 0.11)		0.05 (–0.11, 0.21)	0.04 (–0.12, 0.20)
Ca^{2+} ($mg \cdot L^{-1}$)	L26	2.27 (2.17, 2.37)	–0.18 (–0.34, –0.02)*	–0.12 (–0.64, 0.41)	–0.18 (–0.70, 0.35)	–0.24 (–0.77, 0.28)
	L39	1.59 (1.50, 1.69)	–0.14 (–0.29, 0.02)	–0.08 (–0.33, 0.18)	–0.04 (–0.30, 0.21)	–0.29 (–0.54, –0.04)*
	L42	1.31 (1.23, 1.40)	–0.18 (–0.32, –0.04)*	–0.09 (–0.29, 0.10)	–0.13 (–0.32, 0.06)	–0.32 (–0.51, –0.13)*
Mg^{2+} ($mg \cdot L^{-1}$)	L26	0.50 (0.48, 0.53)	–0.06 (–0.12, –0.01)*	–0.05 (–0.12, 0.03)	–0.12 (–0.19, –0.04)*	–0.03 (–0.11, 0.05)
	L39	0.40 (0.39, 0.42)	–0.06 (–0.10, –0.03)*	–0.03 (–0.09, 0.04)	–0.09 (–0.15, –0.02)*	–0.07 (–0.13, –0.01)*
	L42	0.34 (0.33, 0.36)	–0.05 (–0.09, –0.02)*	–0.02 (–0.07, 0.03)	–0.06 (–0.11, –0.01)*	–0.07 (–0.12, –0.02)*
Na^+ ($mg \cdot L^{-1}$)	L26	0.96 (0.89, 1.03)	0.05 (–0.06, 0.16)	–0.00 (–0.22, 0.21)	–0.01 (–0.22, 0.21)	0.16 (–0.06, 0.37)
	L39	0.75 (0.73, 0.78)	–0.00 (–0.04, 0.03)	–0.02 (–0.13, 0.09)	0.01 (–0.11, 0.12)	0.01 (–0.11, 0.12)
	L42	0.58 (0.57, 0.60)	0.01 (–0.02, 0.03)	0.01 (–0.08, 0.11)	0.00 (–0.09, 0.10)	–0.00 (–0.10, 0.10)
SO_4^{2-} ($mg \cdot L^{-1}$)	L26	2.57 (2.41, 2.74)	–0.12 (–0.43, 0.20)		–0.08 (–0.78, 0.62)	–0.15 (–0.85, 0.55)
	L39	2.57 (2.40, 2.74)	–0.06 (–0.38, 0.25)		0.02 (–0.66, 0.69)	–0.14 (–0.82, 0.53)
	L42	2.67 (2.38, 2.97)	0.00 (–0.55, 0.56)		0.33 (–0.40, 1.07)	–0.33 (–1.06, 0.40)
Cl^- ($mg \cdot L^{-1}$)	L26	0.19 (0.18, 0.21)	0.03 (0.01, 0.05)*	0.04 (–0.04, 0.12)	0.02 (–0.05, 0.10)	0.03 (–0.04, 0.11)
	L39	0.17 (0.15, 0.20)	0.04 (0.00, 0.08)*	0.02 (–0.10, 0.15)	0.03 (–0.09, 0.15)	0.07 (–0.05, 0.19)
	L42	0.16 (0.14, 0.19)	0.03 (–0.01, 0.06)	0.01 (–0.09, 0.10)	0.03 (–0.07, 0.13)	0.05 (–0.05, 0.14)
Si ($mg \cdot L^{-1}$)	L26	1.17 (1.10, 1.23)	0.08 (–0.03, 0.18)	0.04 (–0.22, 0.29)	0.17 (–0.09, 0.43)	0.03 (–0.23, 0.29)
	L39	0.52 (0.43, 0.60)	0.09 (–0.05, 0.23)	0.14 (–0.33, 0.61)	0.07 (–0.40, 0.55)	0.04 (–0.43, 0.51)
	L42	0.03 (0.0, 0.07)	0.06 (0.01, 0.11)*	0.01 (–0.07, 0.09)	0.10 (0.02, 0.18)*	0.08 (0.00, 0.16)*

Note: Annual means and differences were estimated by RM-ANOVA. The 95% confidence limits are given in parentheses. Asterisks identify differences where the 95% confidence interval does not span zero. The prelogging period was 1993–1995 for conductance and 1991–1994 for L39 K^+; the postlogging period was 1998–1999 for pH, TP, TN, K^+, and SO_4^{2-}. Chl *a* data were June–September measurements, with a prelogging period of 1992–1995.

[a]Based on one August measurement.

[b]Pre- and post-logging differences based on epilimnetic observations, usually means of 0.5- and 5.5-m samples: L26 data were July, August, and September measurements, L39 data were June, July, and September measurements, and L42 data were June–September measurements.

suppression and riparian management policies have the potential to produce shoreline forests dominated by narrow strips of shade-tolerant tree species unrepresentative of natural boreal forest conditions. In situations where shoreline buffer strips are not required for other purposes, there may be potential to harvest and regenerate shoreline forest, provided sedimentation associated with roads is effectively controlled through modern design practices (Moore 1983). As

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part of a landscape-scale forest management design, this may lead to creation of complex shoreline disturbance histories more consistent with historical fire disturbance patterns. Experiments or adaptive management initiatives designed to test this approach seem unlikely to cause harmful alteration of lake water quality.

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Effects of forestry roads on reproductive habitat and exploitation of lake trout (*Salvelinus namaycush*) in three experimental lakes

John M. Gunn and Rod Sein

Abstract: This study was designed to test the effects of two potential impacts of forest access roads on lake trout (*Salvelinus namaycush*) lakes in the Boreal Shield ecozone: (*i*) loss of reproductive habitat through siltation and (*ii*) increased access and exploitation. During an 9-year study (1991–1999) in Whitepine Lake, access to seven original spawning sites and over 250 alternate spawning sites was progressively removed by covering the substrate with opaque plastic sheeting to simulate siltation. No effects on recruitment of lake trout have yet been detected. Mark–recapture estimates of juvenile (<370 mm fork length) abundance remained high, mean body size did not increase, and emergent alevins continued to be produced from the alternate spawning sites each year. Similar results occurred in a short-term study in Helen Lake. The lack of obvious effects of reproductive habitat loss was in sharp contrast with the rapid and severe effects that fishing pressure exerted on the lake trout population in Michaud Lake where access was improved by construction of a 12-km forest access road. These findings suggest that lake trout can tolerate substantial losses in spawning habitat, but natural populations, particularly in small lakes, must be protected from excessive exploitation.

Résumé : Notre étude visait à tester les effets de deux impacts potentiels des routes forestières sur les lacs à touladi (*Salvelinus namaycush*) de l'écozone du bouclier boréal : (*i*) perte d'habitat de fraye par colmatage, et (*ii*) augmentation de l'accès et de l'exploitation. Pendant une étude de 9 ans (1991–1999) menée au lac Whitepine, nous avons progressivement limité l'accès à sept frayères établies et à 250 frayères de substitution en couvrant le substrat de feuilles de plastique opaque simulant le colmatage. Nous n'avons pour le moment détecté aucun effet sur le recrutement du touladi. D'après des estimations obtenues par marquage–recapture, l'abondance des juvéniles (<370 mm de longueur à la fourche) est demeurée élevée, la taille corporelle moyenne n'a pas augmenté, et des alevins nageants continuaient à être produits par les frayères de substitution chaque année. Des résultats similaires ont été obtenus par une étude de courte durée menée au lac Helen. L'absence d'effets évidents par perte d'habitat de fraye contraste fortement avec les effets dévastateurs exercés par la pression de pêche sur la population de touladi du lac Michaud, où l'accès a été amélioré par la construction d'une route forestière de 12 km. Ces résultats permettent de penser que le touladi peut tolérer des pertes importantes d'habitat de fraye, mais que les populations naturelles, particulièrement dans les petits lacs, doivent être protégées contre une exploitation excessive.

[Traduit par la Rédaction]

Introduction

Extensive erosion and sediment input to lakes and streams can occur from poorly engineered roads and bridge approaches or from improperly installed culverts (Megahan and Kidd 1972; Plamondon 1982; Anderson and Potts 1987). If the roads and stream crossings are not properly maintained, the adverse effects can continue well after initial road construction. In the longer term, if access roads are left open to vehicle traffic, they will frequently lead to changing human use patterns of the area. Increased exploitation of fish populations, intentional and unintentional introduction of exotic species, and development of shorelines for cottages are some of the many changes likely to occur as remote areas are opened up by roads (Schindler 1998).

There are now very few parts of Ontario's Boreal Shield landscapes that are remote from access roads (Fig. 1). This network of roads and associated human-directed impacts represents a largely unplanned legacy from forestry, mining, and other resource extraction industries. However, to date, there have been few attempts, particularly in the Boreal Shield ecozone of Canada, to measure the impacts of road-related effects on aquatic ecosystems. To do this, we adopted an experimental manipulation approach to test and compare two potential effects of forest access roads on fish populations: sedimentation and excessive exploitation.

We concentrated our studies on small lakes that supported naturally reproducing populations of lake trout (*Salvelinus namaycush*), a species that receives special attention in forestry management plans, particularly in Ontario (Ontario Ministry of Natural Resources 1988). Less than 1% of Ontario's lakes contain this prized sport fish species (Martin

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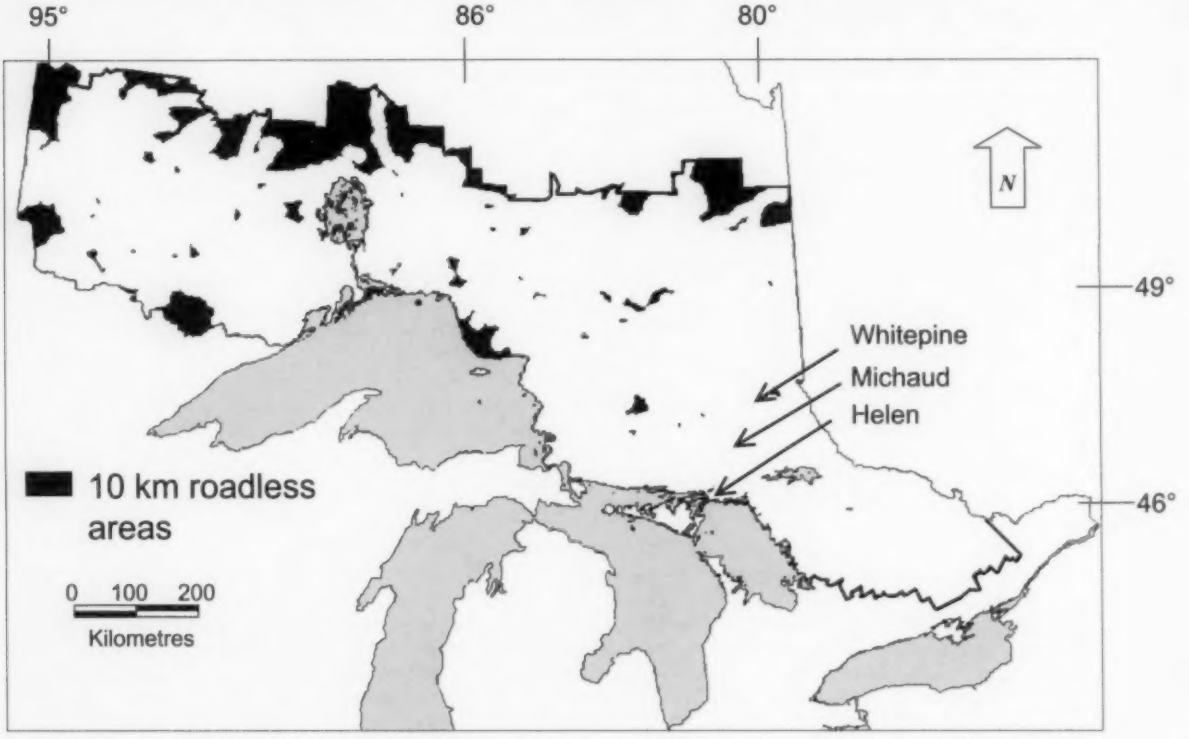
Fig. 1. Areas within the outlined Boreal Shield landscape of Ontario, Canada, that are >10 km from roads. Data provided by Ontario Ministry of Natural Resources. The locations of our study lakes are indicated.



and Olver 1976), and lake trout are considered to be highly sensitive to the disturbances that often accompany forestry operations. Under current guidelines in Ontario (Ontario Ministry of Natural Resources 1988), all lake trout lakes must have 30- to 90-m terrestrial buffer strips (depending on slopes) left around the entire shoreline, within which no road construction or tree harvesting is allowed. Road crossings of streams as potential point sources of sediment appear to represent more of a threat to nearshore spawning habitat of lake trout than silt inputs from clearcut logging areas. Clearcut areas in the low-relief landscape of much of the boreal forest appear to have little, and probably quite temporary, effects on sediment transport to lakes (Blais et al. 1998; Steedman and France 2000).

Spawning sites are identified as "critical fish habitat" in the guidelines and are considered essential areas that must be protected from sedimentation (Ontario Ministry of Natural Resources 1988). The reproductive habitat is considered particularly vulnerable because the lake trout is a demersal spawner that broadcasts its eggs over clean coarse substrates in very shallow (<2 m deep) nearshore (<10 m from shore) waters in small shield lakes (Martin 1957; DeRoche 1969; Gunn 1995). The developing embryos are deep in the interstitial spaces of the substrate for nearly 7 months (October–April) and can readily be suffocated by sediments eroding from the catchment (Sly and Evans 1996).

Ontario forestry guidelines and management plans usually give inadequate consideration to the very low productivity and high exploitation vulnerability typical of lake trout lakes (Ryder and Johnson 1972; Shuter et al. 1998). Estimates of the sustainable harvest levels for lake trout populations are usually <1 kg·ha^{-1}·year^{-1} (Healey 1978; Martin and Olver 1980). Shuter et al. (1998), using a simulation model that they developed, predict that small (100 ha) lakes on the shield are more productive (maximum sustainable harvest of approximately 1.5 kg lake trout·ha^{-1}·year^{-1}) than larger (1000, 10 000 ha) lakes but are extremely vulnerable to overfishing. They estimated that small lakes may not be able to sustain more than approximately 7 h fishing effort·ha^{-1}·year^{-1} (Shuter et al. 1998).

For our experiments, we used three small lakes to test the effects of spawning habitat loss and exploitation on lake trout populations. In the first lake, Whitepine Lake, we used opaque plastic sheeting and progressively covered, during 1992–1999, available nearshore spawning habitat to simulate the effect of a sediment discharge to the lake. A second lake, Helen Lake, was added to the study in 1999 to verify the results of the habitat manipulation experiment using a lake with a more complex fish community. In the third lake, Michaud Lake, we assessed the effects of exploitation on a remote lake when fishing resumed after a 7-year closure period, 1991–1997. Improved access to the lake was provided by the construction of a forest access road in 1994.

Methods

The three study lakes are all small (67–148 ha) headwater lakes located 40–90 km from Sudbury, Ontario (Fig. 1), and are located

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Table 1. Description of the Whitepine Lake and Helen Lake lake trout spawning sites.

	Spawning sites used		Site characteristics				Spawning habitat covered		
Year	Number	Total area (m^2)	Surface area (m^2)	Water depth (m)	Distance from shore (m)	% of sites producing alevins	Egg deposition area (m^2)	Adjoining areas (m^2)	Total (m^2)
Whitepine Lake									
1991	7	40	0.5–21.0	0.3–1.5	1.4–4.5	na	0	0	0
1992	15	74.8	0.5–21.0	0.2–2.0	na	na	6	86	92
1993	18	64.9	0.5–21.0	0.1–1.2	na	44.4	13	86	99
1994	41	40.3	0.1–5.0	0.1–2.0	0.5–4.0	na	21	71	92
1995	44	82.7	0.2–10.0	0.3–0.8	0.3–0.9	na	6	0	6
1996	39	195.3	0.9–42.0	0.1–1.5	0.4–2.7	76.9	189	101.6	290.6
1997	52	126.3	0.1–15.0	0.1–1.4	0.4–6.0	44.3	195.3	28.4	223.7
1998	41	226.4	0.1–78.9	0.2–1.3	0.8–6.0	46.3	126.3	68.9	195.2
1999	41	98.1	0.1–13.2	0.2–1.5	0.2–15.0	51.2	226.4	378.6	605
Helen Lake									
1997	5	11.5	0.2–9.0	0.5–0.7	na	40	0	0	0
1999	9	44.2	0.2–15.0	0.3–0.8	na	55.5	11.5	138.5	150

Note: Spawning sites are defined as the area of egg deposition during the fall spawning period. Substrates are inspected immediately after ice-off in April and early May to identify spawning sites that produced alevins. On Whitepine Lake, the traditional spawning sites were gradually covered with plastic sheeting during 1992–1994. During 1996–1999 (Whitepine Lake) and 1999 (Helen Lake), all previous spawning sites were covered each year.

within the Boreal Shield ecozone. The two principal study lakes, Whitepine and Michaud, have very simple fish communities dominated by small-bodied lake trout, typical of populations with a planktivorous or insectivorous diet. Other species present include yellow perch (*Perca flavescens*), Iowa darter (*Etheostoma exile*), and white sucker (*Catostomus commersoni*) and a few species of cyprinids. The lakes had previously been used in a variety of acid rain related research projects (Gunn and Keller 1984, 1990; Gunn et al. 1987) and had very similar histories. In the early 1980s, they were both acidified (pH < 5.5) and their native lake trout populations were reduced to small remnant stocks of nonreproducing adults. Water quality improved throughout the 1980s because of reductions in emissions of SO_2 in Canada and the United States (Gunn and Keller 1990). Both lakes were stocked with hatchery-reared lake trout to assist in rehabilitation. In Whitepine Lake, the hatchery stocking only occurred in 1980 and 1981 and then was stopped because the native population resumed reproduction in 1982. Reproduction occurred yearly thereafter and a dense population of lake trout developed in Whitepine Lake by 1990. In Michaud Lake, the native fish disappeared before natural recruitment resumed and the hatchery stocking that began in 1984 was maintained periodically until 1992. Natural reproduction of the hatchery fish in Michaud Lake began in 1990. A permanent sanctuary status was established for Whitepine Lake in 1980 to prevent angling exploitation. On Michaud Lake, a temporary angling closure (1991–1997) was established.

Helen Lake (46°06′N, 81°33′W, 41.2 m maximum depth, 20.5 m mean depth) was a nearly pristine lake located within the wilderness setting of Killarney Provincial Park and was used as an alternate lake to test the habitat manipulation technique. It has good water quality, a native reproducing lake trout population, and a complex fish community. In addition to lake trout, it contains smallmouth bass (*Micropterus dolomieu*), rock bass (*Ambloplites rupestris*), cisco (*Coregonus artedi*), brown bullhead (*Ameiurus nebulosus*), bluegill (*Lepomis macrochirus*), pumpkinseed (*Lepomis gibbosus*), yellow perch, slimy sculpin (*Cottus cognatus*), Iowa darter, and bluntnose minnow (*Pimephales notatus*). Helen Lake is open to angling, but angling pressure is quite low because of its location and the fact that motorized access is prohibited.

Whitepine Lake: habitat loss experiment

Whitepine Lake was used as the principal experimental lake to test the hypothesis that spawning habitat reduction in shoreline areas would lead to recruitment failures in native lake trout populations. Previous publications from this experiment dealt with the behavioural response of fish to the habitat disturbances (McAughey and Gunn 1995) and the accuracy of visual techniques of classifying spawning habitat (Gunn et al. 1996).

Whitepine Lake (47°17′N, 80°50′W) is a 67-ha lake (22 m maximum depth, 5.9 m mean depth) with a 4.7-km shoreline. It has a 328-ha terrestrial catchment area consisting of thin sandy soil over granitic bedrock with a few small wetland areas. The area was logged in the past and approximately 30% of the catchment was burned in 1975. At the start of this experiment in 1991, the forest cover was dominated by eastern white pine (*Pinus strobus*) except for the burned area where an early successional mixed cover existed. A band of trees and shrubs occurred along almost the entire shoreline and there was no evidence of severe water level fluctuations or excessive erosion or siltation. Few human disturbances existed in the area. Our small research cabin is the only building in the catchment area.

The habitat manipulation experiment began in October 1991 by mapping all of the traditional spawning sites used by lake trout. Spawning fish were located by cruising the entire shoreline each night of the spawning season (duration of 10–20 days in October) and spotting, with the aid of flashlights, spawning groups of lake trout over shallow (<2 m) nearshore areas of clean coarse substrate. Associated studies have shown that lake trout select 2- to 10-cm-diameter substrate in this lake (Gunn 1995). Identified sites were later confirmed by examining the substrate for the presence of deposited eggs. In 1991 and 1992, egg deposition rates were measured using funnel collectors buried in the substrate (Gunn 1995). In subsequent years, only the presence or absence of eggs was recorded. Frequent searches by boat and by diving eliminated the possibility that there were any offshore sites that went undetected in this study. This was also confirmed by tracking spawning fish tagged with ultrasonic transmitters (J.M. Gunn, unpublished data).

The habitat manipulation began in 1992 by covering the spawning substrate with opaque plastic sheeting, which was left in place throughout the entire period of the experiment. The original spawning sites (seven sites, total surface area 40 m^2) were removed as follows: 15% by area in 1992, 35% in 1993, and 50% in 1994. Testing of the manipulation technique was done in 1995 by covering six previously used sites with sand as a more "natural" distur-

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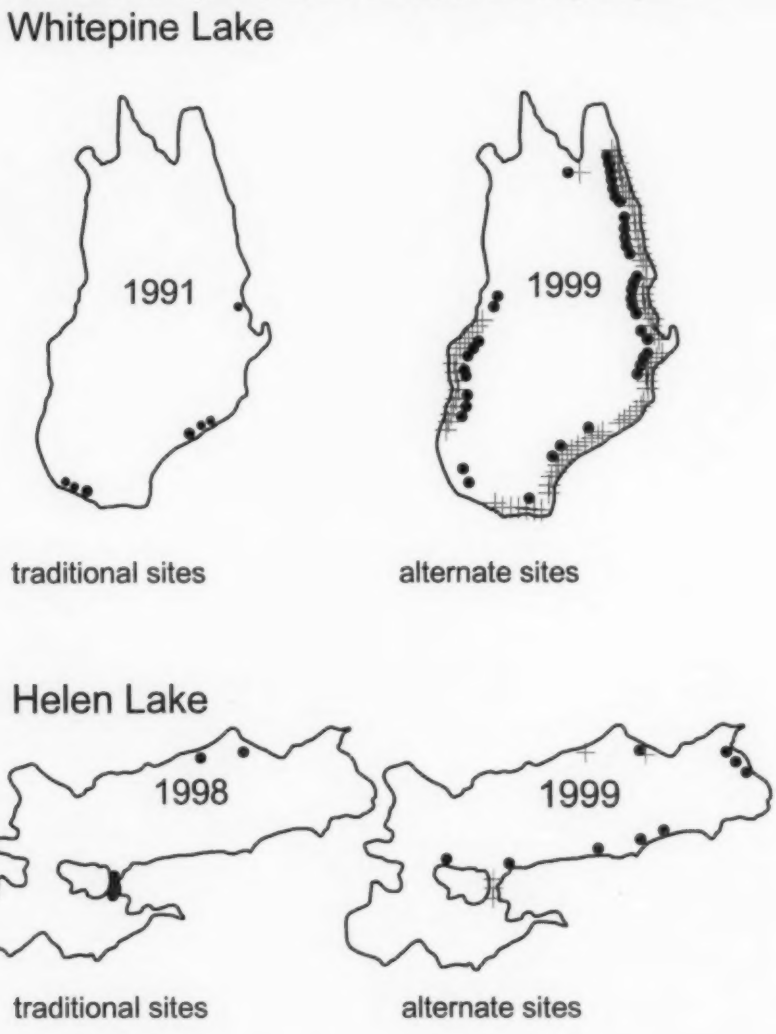
Fig. 2. Locations of traditional lake trout spawning sites and the spawning sites used after the habitat manipulation experiment was completed in Whitepine Lake (1991, 1999) and Helen Lake (1998, 1999). The locations of spawning sites that were covered for this experiment are indicated. Circles denote active spawning sites and crosses denote covered spawning sites.



bance. Fish avoided both the plastic sheeting and the sand-covered sites. Therefore, only the plastic sheeting method was used to cover spawning sites in 1996, 1997, and 1998. In addition to the annual assessment of spawning activity described above, we conducted detailed studies of annual abundance and size structure of the population. Population estimates were conducted in the spring (water temperature 6–15°C) by the continuous mark–recapture Schnabel method (Ricker 1975). Fish were captured by angling or by using short-duration (30 min) sets of small-mesh (38–51 mm stretched mesh) gill nets, and low handling mortality was confirmed through holding experiments (McAughey and Gunn 1995). Accurate age assessment of the fish using otoliths was not possible because of the impact that lethal sampling for aging structures might cause. Instead, estimates of juvenile (<370 mm) abundance were made in terms of body size, based on the assumption that the size-at-maturity relationships observed during the 1994 (Gunn et al. 1996) and 1997 spawning assessments applied throughout. To eliminate resampling the same fish, all captured and released juveniles were given a permanent adipose clip mark. To make sure that a year-class failure did not go undetected, we attempted to capture and mark at least 100 juveniles each year.

The physical characteristics (depth, distance from shore, substrate size, and depth of interstitial spaces) of all new spawning sites were measured shortly after egg deposition ended. The location of the eggs was marked with a numbered brick and a qualitative assessment of overwinter survival was then conducted by divers in late April – early May by excavating the sites and noting the presence or absence of live alevins.

Helen Lake: verification study

A test of the habitat manipulation technique was conducted in Helen Lake in 1999 to verify that the results in Whitepine Lake were not site specific or related to the absence of potential egg predators in the principal study site. Traditional spawning sites on Helen Lake were mapped in 1997 and 1998. In 1999, all five tradi-

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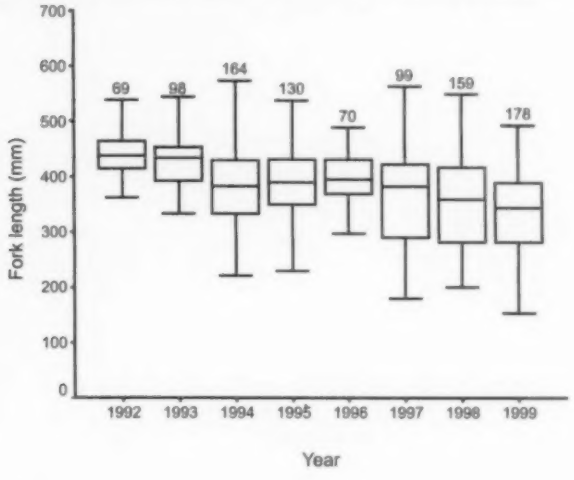
Fig. 3. Size of lake trout captured in the index gill nets in Whitepine Lake, 1991–1999. Annual median, 25th percentile, 75th percentile, maximum, minimum, and sample size are indicated.



tional spawning sites were covered with plastic sheeting and the newly selected sites were located, marked, and assessed for alevin survival following the methods described above.

Michaud Lake: exploitation study

The exploitation experiment involved the assessment of the immediate impact of anglers on a remote lake, Michaud Lake, following construction of a forest access road and the lifting of the fishing ban. The final 12 km of a 26-km forest access road to Michaud Lake (46°49′N, 81°18′W, 148 ha, 24 m maximum depth, 7.0 m mean depth) was completed in 1994, providing access for snow machines and four-wheel-drive vehicles to within 100 m of the lake. In the summer of 1997, a netting survey was conducted to assess the relative abundance of lake trout in the lake. In the fall (October 1–30, 1997), a spawning assessment of adult lake trout in Michaud Lake was conducted and 220 adults were fin marked and released. On January 1, 1998, the fishing season opened under the standard regulations (unlimited entry and access, daily possession limit of three lake trout per angler). No attempt was made to encourage fishing on the lake. There were no public notices in newspapers or elsewhere (the published regulations were actually in error and still indicated that the lake was closed to fishing), and there were no road signs to assist in locating the lake among the many other lakes and forest roads in the area. The newly constructed road was not plowed, so anglers had to use snowmobiles for the final 12 km to reach the lake. Once the fishing began, a random stratified (by weekday or weekend day) creel survey was conducted to assess angling effort and harvest. The creel survey was maintained throughout the winter and early spring of 1998. Netting and spawning surveys were repeated in the summer and fall of 1998 to assess the effects of angling on the lake trout population.

Results and discussion

Habitat loss experiment: spawning site selection and quality

Lake trout proved to be highly adaptable to spawning habitat disturbances and repeatedly selected new sites in Whitepine Lake when previous spawning sites were covered. Similar results were found in Helen Lake where nine new

Table 2. Estimated abundance of juvenile (260–370 mm) lake trout in Whitepine Lake from the springtime surveys.

Year	Number marked	% recaptured	Estimated total number
1992	17	0	—
1993	63	22	180 (118–377)
1994	110	19	406 (284–709)
1995	77	10	507 (300–1653)
1996	45	16	169 (97–653)
1997	75	13	357 (220–938)
1998	89	6	955 (509–7738)
1999	139	9	1013 (647–2332)

Note: Abundance was estimated by Schnabel continuous mark–recapture of angled and gillnetted fish. Estimated number with 95% CI in parentheses is presented.

sites were selected after the traditional sites were covered (Table 1; Fig. 2). In total, over 250 new spawning sites were selected in Whitepine Lake as a result of our experimental manipulations (Table 1; Fig. 2). The accumulated impact of removing access to over 1600 m^2 of substrate during this 9-year experiment in Whitepine Lake did not prevent fish from spawning; however, it did appear to represent a severe enough impact that fish were forced to select what appeared to be marginal habitat. All the newly selected spawning sites in Whitepine Lake had at least a small patch of substrate within the preferred range (2–10 cm in diameter), but many of the sites were very small (<0.2 m^2 surface area), had limited interstitial space beneath the substrate for eggs to settle in, and were in shallow water (<0.4 m) where eggs appeared to be highly vulnerable to both predation and ice damage (Table 1). In the few relatively large sites, eggs were thinly dispersed and appeared to have drifted considerable distances before they became wedged within the substrate. The large number of widely dispersed sites (Fig. 3) was further evidence of the severe disturbance imposed by the habitat removal. Lake trout usually spawn in mass at relatively few sites (Martin 1957; DeRoche 1969; Gunn 1995). It is rare to find an inland lake trout lake with more than 10 traditional spawning sites, including lakes much larger than Whitepine Lake (McMurtry 1986).

In the early years of the study, the lake trout exhibited strong fidelity to the seven traditional sites (Gunn 1995; McAughey and Gunn 1995). However, as the study proceeded, it became evident that prior experience with a site proved unnecessary. Learned behaviours or chemosensory cues from previous use of a site (Foster 1985; Hara 1994) may assist a fish in returning to a site, but our study shows that the innate behaviour of being able to readily identify useable habitat is very powerful in this species.

Evidence of recruitment failure

We were not able to accurately quantify egg deposition rate or survival rates of incubating embryos, but the new sites continued to produce alevins each year (Table 1), demonstrating that recruitment was not eliminated by the habitat disturbances. For example, in the final year of the study, 21 of the 41 sites (51.2%) on Whitepine Lake contained live alevins on May 2, 2000. The presence of live alevins in the majority of the sites on Whitepine Lake occurred even though the amount of potential habitat lost during the experi-

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Fig. 4. Weekly estimates of the number of anglers (bars), fish captured per angler-hour (thin line), and accumulated harvest of lake trout (thick line) in Michaud Lake during the winter and spring of 1998, the year the lake opened to fishing.

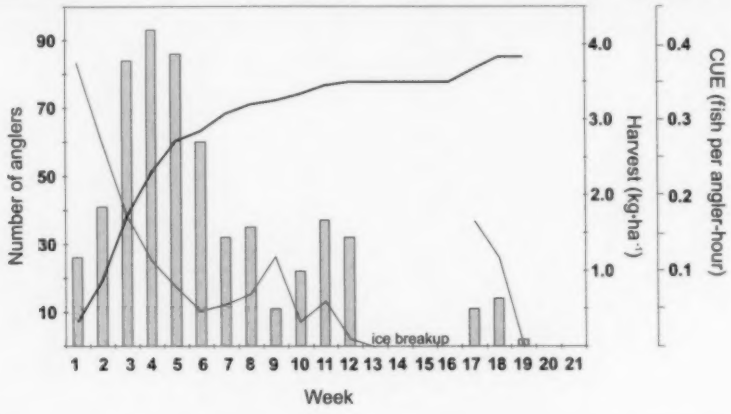

Table 3. Effects of 1998 winter fishing on abundance of lake trout in Michaud Lake.

Year	Date	Number of net sets	Lake trout catch
1997	August 6–12	60	1.23 (1.33)
1998	August 12–19	60	0.37 (0.90)

Note: The population was assessed using multimesh gill nets (15-m single panels of 19-, 25-, 38-, 51-, and 64-mm stretched mesh with 5-m spacers between panels) set at random locations within the hypolimnion. The lake trout catch is the number of fish captured during a 2-h net set. Mean with 1 SD in parentheses is given.

ment was more than 40 times that of the original area of substrate that supported the population in 1991. Similar results occurred in the 1-year manipulation of Helen Lake where five of nine (55.5%) newly selected sites contained alevins on April 18, 2000.

The mark–recapture estimates of juvenile abundance on Whitepine Lake also failed to show any of the expected effects of the experimental treatment. We had predicted that juvenile abundance would decline as a result of the habitat loss, expecting the decline to begin soon after all the traditional spawning sites were removed in 1994. The mean size of fish in the index gill nets was also expected to increase with time if abundance of juveniles, and resulting competition for food, declined.

There was no decline in the abundance of juveniles (260–370 mm fork length) detected during the study (Table 2). The average size of fish in the population also did not increase (Fig. 3), giving further evidence that recruitment was unaffected by the habitat loss. Age assessment data are not yet available for fish collected during recent years, but from age–size relationships obtained earlier (Gunn et al. 1996), it is clear that most of the abundant juveniles in Whitepine Lake are recruits from the new spawning sites. The difficulty in capturing very young fish (<3+) with our assessment methods means that year-class declines may still be detected in the future as a result of possible reduction in the survival of the egg to alevin stages in the latter years of the study. However, the continued production of alevins at the alternate sites throughout the study suggests that the habitat manipulations would have to be continued for many more years to be able to detect a complete loss of recruitment.

Exploitation following improved road access

The effects of exploitation on Michaud Lake were not subtle. Anglers were able to access the lake in midwinter by way of the new road. Anglers used snowmobiles and all-terrain four-wheel-drive vehicles to travel right to the lake itself. Catch rates were very high when the fishery opened in the first week of January 1998 (0.4 fish·angler^{-1}·h^{-1}), and most anglers were able to catch their allowable limit of three fish each day (angler-day) (Fig. 4). The number of angler-days increased steadily, reaching a maximum of 93 in the fourth week of January.

The sustainable yield level (kilograms per hectare) for Michaud Lake, a 148-ha lake, was estimated to be 1.35 kg·ha^{-1} from the following equation of Payne et al. (1990):

$$\log_{10}(\text{harvest}) = 0.50 + 0.83\log_{10}(\text{area}).$$

The estimated maximum sustainable yield level was exceeded less than 3 weeks after anglers accessed the lake (Fig. 4). Fishing success rate declined through the winter, but anglers continued to harvest lake trout until ice melt forced an end to the fishery. Once the road was dry enough to permit truck travel, anglers brought boats to the lake and began fishing again on April 24, 1998. Fishing success rates improved for a brief period in the open-water period but declined rapidly. Anglers largely abandoned the lake in early May.

In this brief fishery, the estimated harvest reached 3.8 kg·ha^{-1} in less than 5 months. The creel survey crews observed a total of 395 harvested fish. Twenty-two percent of the creel survey sample was fin clipped, providing a mark–recapture estimate of 765 (95% CI = 607–963) for the pre-angling adult portion of the population. This population was reduced by approximately 72% (final population estimate 210 (95% CI = 52–408) in the winter and spring fishery. The midsummer index netting survey provided consistent evidence of the population decline. Average catch rates of lake trout declined by 70% between 1997 and 1998 (Table 3).

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In conclusion, the results of this study suggest that lake trout are not particularly vulnerable to damage from the physical alterations to spawning habitat that may occur through the construction of forest access roads in Boreal Shield areas of Ontario. First, there are management guidelines in place (e.g., Ontario Ministry of Natural Resources 1988, 1990, 1991) for the construction of roads that, if followed, should limit siltation of streambeds and inlet areas of lakes. Unlike other *Salvelinus* species such as brook trout (*Salvelinus fontinalis*) (Curry et al. 1997; Curry and Devito 2000), lake trout appear to rarely if ever use streams or the area immediately adjoining inlet streams for spawning. In a survey of 95 lake trout lakes, McMurtry (1986) found that no lake trout spawning sites were within 20 m of a stream inlet. Our study shows that if siltation of shorelines did actually occur, lake trout would seek spawning sites elsewhere and could maintain recruitment at these alternate sites. Siltation events would have to be extremely extensive and long-lasting to completely eliminate reproduction in this long-lived species.

The fact that we have not yet detected a substantial effect of progressive spawning habitat loss on lake trout recruitment in two experimental lakes does not mean that there is an unlimited supply of suitable spawning habitat on shield lakes or that lake managers should be any less diligent about protecting fish habitat from disturbances. Spawning habitat loss is surely one of a suite of stressors that have a cumulative effect on lake trout. However, our experimental results clearly suggest that resource managers need to question whether fish harvest controls and improved motor vehicle access to lake trout lakes have received sufficient attention in forest and fisheries management planning. We think that forest access roads and the increases in angling pressure that they create have a far greater impact on Boreal Shield lake trout populations than spawning habitat loss due to sedimentation.

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Comparative impacts of fire and forest harvesting on water quality in Boreal Shield lakes

Richard Carignan, Pierre D'Arcy, and Sébastien Lamontagne

Abstract: Water quality was monitored in Boreal Shield lakes for 3 years following their simultaneous impact by clearcut logging or wildfire. Seventeen similar undisturbed lakes served as references. Dissolved organic carbon (DOC) and the light attenuation coefficient (ε_{PAR}) were up to threefold higher in cut lakes than in reference and burnt lakes. Compared with median values for reference lakes, cut and burnt lakes had higher concentrations of total phosphorus (TP) (two- to three-fold), total organic nitrogen (TON) (twofold), and K^+, Cl^-, and Ca^{2+} (up to sixfold). NO_3^- and SO_4^{2-} concentrations were up to 60- and 6-fold higher, respectively, in burnt lakes than in reference and cut lakes. In most cases, impacts were directly proportional to the area harvested or burnt divided by the lake's volume or area. These simple models correctly predicted the changes observed in three lakes harvested during the study. Some of the observed effects occur on different time scales. Mobile ions released by fire (K^+, Cl^-, SO_4^{2-}, NO_3^-) or harvesting (K^+, Cl^-, some DOC) are rapidly flushed out of the watershed (50% decrease in 3 years). Other constituents or properties (TP, TON, DOC, ε_{PAR}, Ca^{2+}, Mg^{2+}) show little change or are still increasing after 3 years and will take a longer time to reach normal levels.

Résumé : Nous avons mesuré la qualité des eaux dans plusieurs lacs du bouclier canadien pendant trois années suivant leur impact par la coupe à blanc ou par des feux de forêt. Dix-sept lacs vierges semblables servirent de témoins. Les concentrations en carbone organique dissous (COD) et le coefficient d'atténuation lumineuse (ε_{PAR}) étaient deux à trois fois plus élevés dans les lacs coupés que dans les lacs brûlés. Par rapport aux valeurs médianes observées dans les lacs témoins, les lacs coupés et brûlés avaient des concentrations de deux à trois fois plus élevées en phosphore total (PT), deux fois plus élevées en azote organique total (NOT) et jusqu'à six fois plus élevées en K^+, Cl^- et Ca^{2+}. Le NO_3^- et le SO_4^{2-} étaient respectivement 60 et six fois plus élevés dans les lacs brûlés que dans les lacs coupés et les témoins. Dans les lacs brûlés et coupés, la majorité des impacts étaient directement proportionnels au rapport entre la superficie déboisée et la superficie ou le volume du lac récepteur. Ces modèles simples ont prédit correctement les effets observés dans les lacs déboisés pendant l'étude. Les effets observés se déroulent sur des échelles temporelles différentes. Les ions mobiles minéralisés par le feu (K^+, Cl^-, SO_4^{2-}, NO_3^-) ou relâchés après coupe (K^+, Cl^-, du COD) ainsi qu'une partie du COD sont rapidement (50% en 3 ans) lessivés du bassin-versant. Les autres substances ou propriétés (PT, NOT, DOC, ε_{PAR}, Ca^{2+}, Mg^{2+}) ont peu changé ou augmentent encore après 3 ans et prendront plus de temps à revenir à des valeurs normales.

Introduction

Aquatic ecosystems of the Canadian boreal forest are influenced by recurring (50–300 years) wildfires that annually cover from less than 0.1 to 1.0% of the land surface (Natural Resources Canada 1996). During the last century, forest harvesting has increased to such an extent that it now exceeds fire as a disturbance agent in large tracts of the boreal forest, with an annual removal rate reaching 1% in some regions. Boreal forest exploitation is currently shifting towards natural disturbance based models (Hunter 1991, 1993; Franklin 1993). These models propose that fire and logging have similar impacts on ecosystems and that forest exploitation patterns emulating fire should preserve ecosystem integrity. These important assumptions remain largely unverified, however, for both terrestrial and aquatic ecosystems.

Given the diversity in vegetation, landforms, and geology occurring throughout the deciduous, mixed, and boreal forest biomes, relatively few studies have documented the effects of these disturbances on the chemistry and biology of surface waters. Most have described the effects of fire or clearcutting on stream chemistry or hydrology (e.g., Likens et al. 1970; Nicolson et al. 1982; Bayley et al. 1992), while a minority of studies have focused on lakes (Wright 1976; Rask et al. 1993, 1998; Garcia and Carignan 1999). Although coherent models have yet to emerge regarding the impact of either disturbance on surface waters, previous studies have established that the loss of forest cover by fire and clearcuts increases, to varying degrees, runoff and the export of particulate matter, nutrients, major ions, and colour. Few studies were designed, however, to compare the effects of forest removal by fire and clear-cutting or to provide quantitative impact models linking the type and extent of watershed disturbance to water quality in lakes.

During the summer of 1995, four major wildfires totalling

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1620 km^2 occurred in a portion of Québec's boreal forest undergoing extensive harvesting operations. The large number of lakes (~800) simultaneously impacted by fire or harvest provided a unique opportunity to compare and to model the effects of both disturbances on water quality and on biotic communities in similar lakes (see Patoine et al. 2000; Planas et al. 2000; St-Onge and Magnan 2000). The present report compares some of the chemical and physical changes that occurred in the lakes during the first 3 years after impact. A companion paper (Lamontagne et al. 2000) compares element export from the catchments of these lakes.

Methods and materials

Study region

The lakes are located in a 30 000-km^2 area surrounding Gouin Reservoir in Haute-Mauricie, Québec (48°50′N, 75°00′W) (Fig. 1). The region intersects the Grenville and Superior geological provinces of the Canadian Shield. The three dominant rock formations encountered are a gneissic complex rich in quartz, plagioclase, biotite, and horneblende, a granodioritic gneiss, and a mixture of intrusive granodiorites and granites in the Superior province, which crosses the northeast quadrant of the region. The low (40–150 m net elevation) rolling hills are covered by glacial deposits that are generally thin (0–2 m) but that can locally exceed 10 m thick. The forest is mainly composed of black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), jack pine (*Pinus divaricata*), white birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*). Wetlands cover ~10% of the region, which annually receives ~1000 mm of precipitation (40% as snow). Runoff was estimated at 562, 694, and 490 mm in 1996, 1997, and 1998, respectively (Lamontagne et al. 2000). Runoff was high in 1997 and low in 1998 compared with its long-term average of 586 mm.

The fire-impacted lakes are located in two of the four large 1995 wildfire areas, Parent (645 km^2) and Belleplage (406 km^2) (Fig. 1), where fire severity ranged from medium to high. Most of the fire-impacted lakes described below are located in catchments where complete loss of foliage occurred, often with more than 40% of the boles fallen and partially consumed. Less severe crown fires leaving some intact vegetation occurred in 50 and 25% of the catchments of lakes FP2 and FP30, respectively. Little (<5%) or no salvage logging occurred in the watersheds of the study lakes. Clearcuts were of the CPRS type (cut with protection of regeneration and soils). Cut block size generally ranged from 5 to 50 ha but occasionally reached 200 ha, with 20-m buffer strips fringing permanent streams, lakes, and wetlands.

Lake selection

Thirty-eight thermally stratified headwater lakes were selected on the basis of comparable size, basin morphometry, and catchment properties. The lakes formed four groups: 16 reference lakes ("N" lakes), nine burnt lakes, which had most of their catchment burnt in 1995 ("FP" and "FBP" lakes), nine cut lakes, which had 9–72% of their catchment logged in 1995 ("C" lakes), and four lakes that had 5–24% of their catchment logged during the study ("P" lakes). The following criteria were used in the selection process: forest age exceeding 50 years, <6% of catchment occupied by wetlands, drainage ratio (DR) between 2 and 15, hydrological order near 1, maximum depth exceeding 5 m, fetch longer than 1 km, perturbation by fire or logging in 1995, and no salvage logging on burnt catchments.

All retained lakes met these conditions, with the following exceptions. Lakes C43 and N120 had some 40- and 45-year-old tree stands in their catchments. Note that stands aged >70 years on Québec's vegetation maps can be considerably older. Lake order is not always exactly 1, as 17 lakes have smaller lakes in their drainage areas. These smaller lakes represent, on average, only 14% of the surface area of the downstream study lakes. Lake FP15 (48 ha) is an exception and has a much larger (154 ha) headwater lake. Logging operations continued after 1995 in the catchment of Lake C2 where the fraction cleared increased from 31 to 72% from 1995 to 1998. One lake (P107) slated for logging during the study had only 5% of its catchment harvested in 1997–1998 and was treated as a reference lake.

Lake morphometry and catchment properties

Bathymetric maps were established from aerial photographs and from 15–25 echosounder transects. Provincial vegetation and soils maps (1 : 20 000) and a digitizing table were used to measure vegetation composition and age and to estimate the type and thickness of superficial deposits. Provincial topographic maps (1 : 20 000) were used to delineate watersheds and to measure wetland cover. The topography of each drainage area was digitized to produce 10-m-resolution digital elevation models and to measure mean catchment slope (Arc/Info, ESRI). Water residence times were not corrected for increased runoff due to loss of forest cover.

Sampling and chemistry

The lakes were sampled three times each year during the ice-free season (a few days after ice-out in late May or early June, in mid-July, and in mid-September). The penetration of light available to photosynthesis (photosynthetically active radiation (PAR), 400–700 nm) and the PAR extinction coefficient (ε_{PAR}) were measured with Li-Cor LI-190 and LI-192SA sensors. Integrated water samples were taken from the euphotic zone (1% of incident PAR), filtered within 12 h when necessary, and stored at 4°C until analyzed (within 72 h). Samples for dissolved organic carbon (DOC) measurements and occasional colour (absorbance at 440 nm) measurements were filtered on washed Gelman Supor 0.45-µm membranes and kept at 4°C. DOC was measured (Shimadzu TOC-5000) within 72 h by infrared gas analysis after sample acidification and He sparging followed by Pt-catalyzed oxidation at 700°C. In these lakes, DOC concentrations measured with Supor 0.45-µm membranes are identical, within measurement precision, to those obtained with precombusted GF/C filters. Total phosphorus (TP) was measured using the molybdenum blue method (Stainton et al. 1977) after autoclaving 50-mL samples with 0.5 g of potassium persulfate for 1 h at 120°C. NO_3^- and NH_4^+ were measured on filtered samples by automated flow injection analysis (Lachat methods 10-107-04-1-B and 10-107-06-1-F). Total nitrogen (TN) was measured as NO_3^- after alkaline persulfate digestion of 50-mL samples at 120°C (D'Elia et al. 1977). TN was not measured in June and July of 1997. The ions Cl^-, SO_4^{2-}, Ca^{2+}, Mg^{2+}, Na^+, and K^+ were measured by ion chromatography (Dionex DX-500). Alkalinity was measured by Gran titration and pH was measured in the laboratory with a double-junction electrode on air-equilibrated samples.

Data analysis

The significance of between-group (reference, cut, and burnt lakes) differences for a given year was assessed using one-way analysis of variance (ANOVA) with a nonparametric Kruskal–Wallis test when distributions were significantly skewed. Repeated-measures ANOVA (RMA, SAS version 6.12) was used to detect significant differences between seasons and years for individual and paired treatments (reference-cut, reference-burnt). Linear regressions were performed on normalized ($\log_{10}$ transformed) data when the significance of relationships obtained with untransformed data depended on a few extreme observations. A stepwise forward variable selection procedure with an F ratio of 4 was used for multiple regressions. The Kruskal–Wallis test was used to verify that regression residuals were normally distributed. Unless otherwise noted, significance tests and regression parameters are significant

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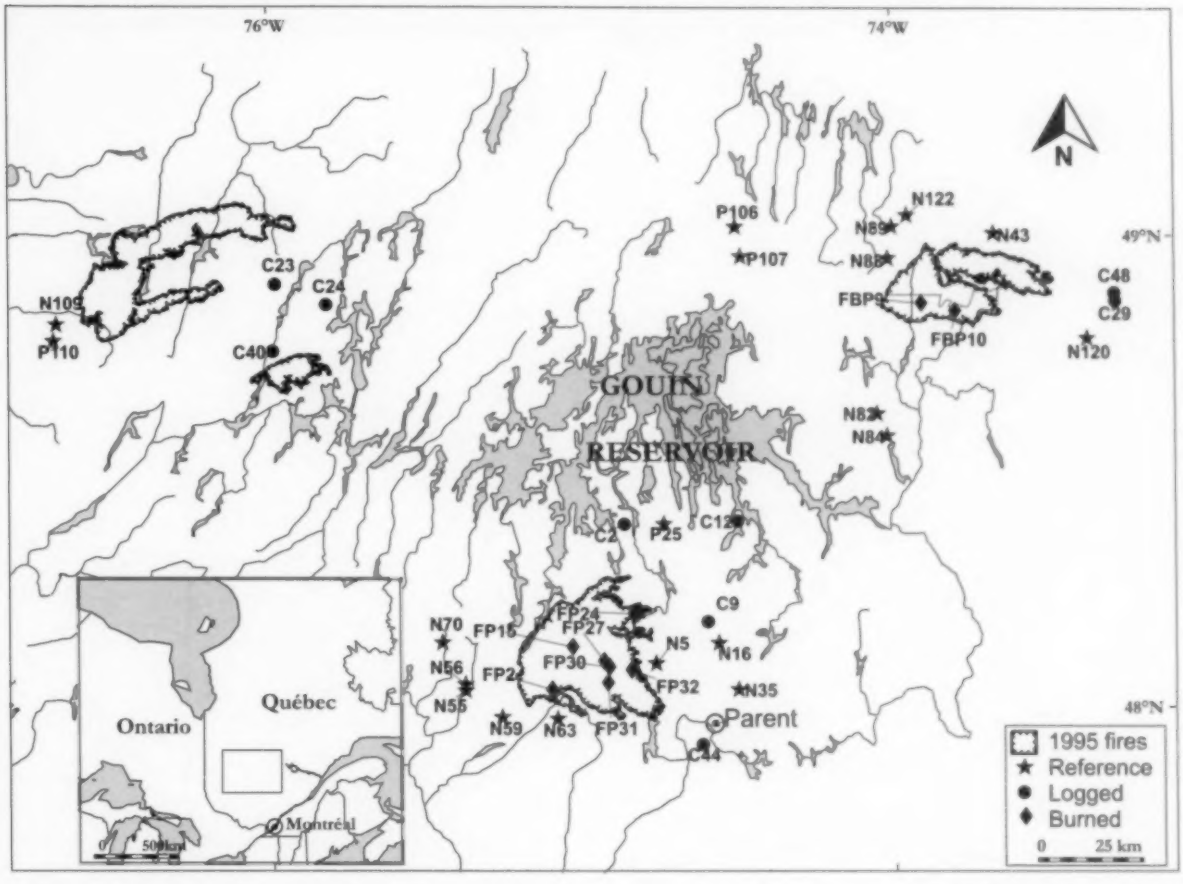
Fig. 1. Map of the study region showing the four 1995 fires and the location of the reference, harvested, and burnt lakes.



at the $p < 0.05$ level. Variable definitions and units are summarized in Table 1.

Results and discussion

Lake morphometry and catchment properties

Several key limnological variables such as DOC, light penetration, and TP are likely to be influenced by morphometric and catchment properties such as the DR, the water residence time, and catchment slope (Schindler 1971; Engstrom 1987; Rasmussen et al. 1989). The four groups of lakes do not differ significantly (ANOVA, $p > 0.05$) with respect to all properties listed in Table 1, with the following exceptions: lakes harvested in 1995 (C lakes) are, on average, located 20 km further north than reference lakes (N lakes), reference lakes tend to be shallower (4.3 versus 5.8 m) than burnt lakes (F lakes), and burnt lakes had less conifers (51.2% of catchment area (CA)) than the three other groups (65.3–74%). The significant difference in mean depth between reference and burnt lakes is due to the inclusion of one particularly deep lake (FBP27, mean depth (ZM) = 10 m) in the group. Note that although the four groups of lakes do not differ significantly with respect to DR, reference lakes have a lower median DR (5.2) than cut (6.8) and burnt (8.7) lakes.

The study lakes are representative of a large number of lakes in the area. A systematic inventory of the 1549 lakes occurring in four quadrants totalling 3350 km^2 located within the study region shows that 30% of the water surface area is composed of lakes having the same range of lake area (LA) as our study lakes (R. Carignan, unpublished data). Our lakes are probably biased towards low DR, however, since lakes occupy 7.5% of the surface area, which implies an average DR of 12.3.

Mean annual chemical properties and ε_{PAR} for reference, cut, and burnt lakes are compared between groups and between years in Fig. 2. In order to increase the homogeneity of the cut lakes group, Lakes C44 and C40, which had only 9 and 11% of their drainage area harvested, respectively, are excluded from these analyses. Of all variables measured, only pH and alkalinity did not show significant differences between groups (Fig. 2, pH and NH_4^+ not shown). In the 38 lakes, pH ranged from 5.7 to 7.2, with a median of 6.6 in 1996. The box plots in Fig. 2 present a useful but somewhat biased overview of the major differences and similarities observed between reference, cut, and burnt lakes. Cut lakes had a smaller average proportion (58%) of their drainage areas cleared compared with burnt lakes (91%). The effects of harvesting and fire shown in Fig. 2 are therefore not directly comparable.

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Table 1. Watershed characteristics and morphometry of the study lakes.

	Reference (n =17)				Harvested (1995, n = 9)				Harvested (1996–1997, n = 4)				Burnt (1995, n = 9)			
Variable	Median	Mean	Min.	Max.	Median	Mean	Min.	Max.	Median	Mean	Min.	Max.	Median	Mean	Min.	Max.
Latitude (LAT)	48.31	48.40	47.93	49.00	48.71	48.52	47.87	48.85	48.82	48.74	48.34	48.97	48.05	48.22	47.99	48.81
Longitude (LONG)	74.57	74.67	73.41	76.71	74.65	74.8	73.32	76.02	74.66	75.14	74.52	76.73	74.95	74.73	73.83	75.13
Altitude (ALT)	442	453	395	558	422	440	394	556	430	434	391	485	468	460	422	497
Catchment area (CA, km^2)*	1.74	2.01	0.45	4.46	2.58	3.44	0.59	10.28	2.47	2.77	1.32	4.82	3.07	4.93	0.57	19.72
Lake area (LA, km^2)	0.35	0.43	0.15	0.81	0.32	0.56	0.18	2.31	0.43	0.50	0.33	0.81	0.36	0.40	0.17	0.64
Total lake are (ΣLA, km^2)	0.35	0.45	0.15	0.98	0.32	0.62	0.20	2.59	0.48	0.52	0.34	0.81	0.41	0.63	0.18	2.03
Watershed area (WA = CA + ΣLA)	2.20	2.46	0.61	4.81	2.89	4.06	0.90	12.87	2.90	3.30	1.76	5.64	3.42	5.55	0.75	21.75
Drainage ratio (DR = CA/ΣLA)	4.42	5.17	2.33	15.38	6.83	6.75	1.96	13.18	5.22	4.99	2.97	6.54	8.70	7.14	2.51	11.64
Mean depth (ZM, m)	4.1	4.3	2.1	8.5	4.6	5.7	4.6	8.9	4.6	4.6	4.6	4.6	5.3	5.8	4.2	10.0
Max. Depth (ZMAX, m)	11	12	7	21	12	14	5	30	12	14	10	23	15	17	10	34
Residence time (τ, years)	1.40	1.64	0.32	4.00	1.07	1.31	0.44	3.22	1.81	1.75	1.29	2.09	0.84	1.59	0.32	5.58
Catchment slope (SLO, degrees)	5.8	6.4	4.0	9.4	4.9	5.3	3.3	10.9	6.8	6.9	5.2	8.9	6.0	6.7	4.4	10.0
Area burnt (FIR, km^2)	0	0	0	0	0	0	0	0	0	0	0	0	**2.31**	**4.64**	**0.58**	19.51
Area logged (CUT, km^2)	0	0	0	0	**0.99**	**1.70**	**0.11**	**7.52**	**0.30**	**0.46**	**0.20**	**1.04**	0	0	0	0
% of CA burnt	0	0	0	0	0	0	0	0	0	0	0	0	**94.6**	**91.3**	**50.1**	**100.0**
% of CA logged	0	0	0	0	**48.3**	**47.0**	**8.5**	**73.2**	**19.9**	**17.4**	**5.9**	**24**	0	0	0	0
% of CA as wetlands	1.7	1.9	0.0	7.0	1.6	2.3	0.0	6.2	1.7	2.3	0.5	5.1	0.5	0.9	0.0	3.6
% of CA as conifer	69.8	65.3	32.3	79.3	75.8	74.0	52.3	87.5	66.3	67.7	52.2	86.1	**51.2**	**51.7**	**28.7**	**81.9**
% of CA as deciduous	27.1	28.8	11.2	65.6	17.3	21.4	12.5	47.2	31.6	29.8	13.9	42.0	**32.5**	**31.0**	**5.7**	**61.3**
Vegetation age (years)			40	>80			50	>90			50	70			50	70

Note: Attributes with significantly different between-group medians are shown in bold.
*The catchment is defined here as the terrestrial portion of the watershed.

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Table 2. Linear regression equations.

No.	Lakes	Year	Model	r^2	SE
1	R	1996–1998	log DOC = – 0.61±0.07 + 0.35±0.10 log DR	0.44	0.09
2	R	1996–1998	log ε_{PAR} = – 0.30±0.06 + 0.42±0.08 log DR	0.65	0.07
3	R + C	1996	DOC = 0.29±0.03 + 0.083±0.017(CA/VOL) + 0.25± 0.03(CUT/VOL)	0.86	0.09
4	R + C	1997	DOC = 0.30±0.03 + 0.073±0.017(CA/VOL) + 0.22±0.03(CUT/VOL)	0.82	0.09
5	R + C	1998	DOC = 0.29±0.03 + 0.076±0.016(CA/VOL) + 0.17±0.03(CUT/VOL)	0.80	0.09
6	R + C	1996	ε_{PAR} = 0.60±0.06 + 0.20±0.03(CA/VOL) + 0.59±0.07(CUT/VOL)	0.90	0.18
7	R + C	1997	ε_{PAR} = 0.72±0.05 + 0.19±0.03(CA/VOL) + 0.49±0.06(CUT/VOL)	0.89	0.17
8	R + C	1998	ε_{PAR} = 0.67±0.06 + 0.21±0.04(CA/VOL) + 0.52±0.07(CUT/VOL)	0.87	0.20
9	R + C	1996	DOC = 0.27±0.05 + 0.027±0.009(DR) + 0.081±0.016(CUT/ΣLA)	0.70	0.13
10	R + C	1997	DOC = 0.29±0.05 + 0.022±0.008(DR) + 0.072±0.015(CUT/ΣLA)	0.66	0.13
11	R + C	1998	DOC = 0.27±0.05 + 0.023±0.008(DR) + 0.057±0.014(CUT/ΣLA)	0.63	0.12
12	R	1996–1998sp	log TP = –0.90±0.05 + 0.25±0.08 log DR – 0.22±0.07 log ΣLA	0.74	0.06
13	R + C	1996–1998sp	TP = 0.18±0.02 + 0.010±0.004(DR) + 0.026±0.007(CUT/ ΣLA)	0.57	0.06
14	R + C	1996–1998sp	TP = 0.19±0.02 + 0.032±0.009(CA/VOL) + 0.074±0.019(CUT/VOL)	0.70	0.05
15	R + F	1996–1998sp	TP = 0.17±0.02 + 0.014±0.003(DR) + 0.028±0.003(FIR/ ΣLA)	0.90	0.05
16	R + F	1996–1998sp	TP = 0.19±0.02 + 0.033±0.010(CA/VOL) + 0.138±0.014(FIR/VOL)	0.86	0.06
17	R + C + F	1996–1998sp	TP = 0.18±0.02 + 0.010±0.003(DR) + 0.031±0.003(CUT + FIR)/ΣLA	0.83	0.06
18	F	1996sp	log NO_3^- = –1.6±0.3 + 1.2±0.2 log(FIR/ΣLA) + 1.6±0.4 log SLO	0.90	0.15
19	R + C	1996	TON = 13.6±0.7 + 1.55±0.39(CA/VOL) + 2.6±0.8(CUT/VOL)	0.68	2.1
20	C	1996	K^+ = 5.5±2.9 + 3.3±1.0(CUT/ΣLA)	0.62	4.5
21	C	1996	Cl^- = 4.0±1.0 + 1.0±0.3(CUT/ΣLA)	0.58	1.6
22	F	1996	K^+ = 12.7±3.7 + 1.4±0.5(FIR/ΣLA)	0.51	4.9
23	F	1996	Cl^- = 6.8±1.7 + 0.61±0.24(FIR/ΣLA)	0.48	2.2
24	C	1996	Ca^{2+} = 31.0±2.2 + 1.9±0.7(CUT/ΣLA)	0.51	3.4
25	R	1996–1998	SO_4^{2-} = –329±90 + 4.7±1.2(LONG)	0.52	4.0
26	R	1996–1998	Alkalinity = 728±236 – 9.2±2.7(LONG)	0.44	9.8

Note: R, reference lakes; C, cut lakes; F, burnt lakes; sp, springtime values only.

DOC and light penetration

In reference lakes, log DOC (3-year averages) was significantly related (r^2 = 0.44) (Table 2, model 1) to log DR, as usually found (Schindler 1971; Engstrom 1987; Rasmussen et al. 1989). A similar but more accurate relationship was found between the 400- to 700-nm light extinction coefficient (log ε_{PAR}) and log DR (r^2 = 0.65) (model 2).

Compared with reference lakes, several cut lakes had higher DOC concentrations and ε_{PAR}, with DOC showing a significant decreasing trend with time (Figs. 2 and 3). DOC concentrations in burnt lakes were intermediate but did not differ significantly from those of reference and cut lakes. In contrast with cut lakes and compared with reference lakes, DOC and ε_{PAR} increased significantly with time in burnt lakes. DOC concentrations showed a significant (RMA, $p < 0.05$) seasonal pattern in the three groups of lakes, with midsummer values rising 5–15% above those of spring and late summer (Fig. 3). The ε_{PAR} was closely related to DOC in the 38 lakes (r^2 = 0.93). Small seasonal variations in DOC were not always reflected in ε_{PAR}, however, particularly in cut lakes (Fig. 3). Factors such as the bleaching of coloured DOC and seasonal variations in the light-absorbing properties of DOC entering the lakes may explain the slight uncoupling observed between ε_{PAR} and DOC. In reference lakes, the average ε_{PAR} was lowest (0.91) in 1996, increased significantly by 10% during the wettest year (1997), and decreased slightly in 1998.

The high DOC concentrations and ε_{PAR} values observed in cut lakes (Figs. 2 and 3) cannot be entirely attributed to their higher median DR (Table 1) compared with reference lakes. Inclusion of the cut lakes on a linear regression plot of DOC versus DR for reference lakes (Fig. 4) shows that Lakes C2, C12, C23, and C24 lie above the model's upper prediction limit (1996 values), whereas Lakes C9, C29, C40, C44, and C48 lie within the model's prediction limits. Lakes within the model's prediction limits either have a low DR or had only a small fraction of their drainage area harvested. Figure 4 suggests that DOC in cut lakes will significantly exceed the range of natural variability only when their DR exceeds about 4 and when more than about 30% of their drainage area has been cleared. The only exception to this rule is Lake C9, which has a DR value of 6.8, with 45% of CA harvested; this lake is deeper and has a longer residence time (1.1 years) than Lakes C2, C12, C23, and C24 (0.4–0.7 year). When ε_{PAR} is plotted as in Fig. 4, similar results are obtained except that this time, Lakes C2 and C48 lie well above the model's upper prediction limit.

Simple relationships exist between DOC, ε_{PAR} in lakes, and the extent of forest removal in their catchments. The best regression found between DOC and harvesting (1996 data) uses the CA/VOL ratio (square metres/cubic metres) plus a volumetric impact ratio, defined as the harvested surface area to lake volume ratio (CUT/VOL (square metres/cubic metres)) and explains 86% of the variability in DOC (Fig. 5; Table 2, model 3). The slope of the impact ratio decreased markedly in subsequent years, as DOC loading to these lakes decreased (models 4 and 5). Similar relationships are also found for ε_{PAR} (models 6–8; Fig. 5), with the important difference that the slope of these models does not decrease as rapidly with time. For management purposes, CUT/VOL can

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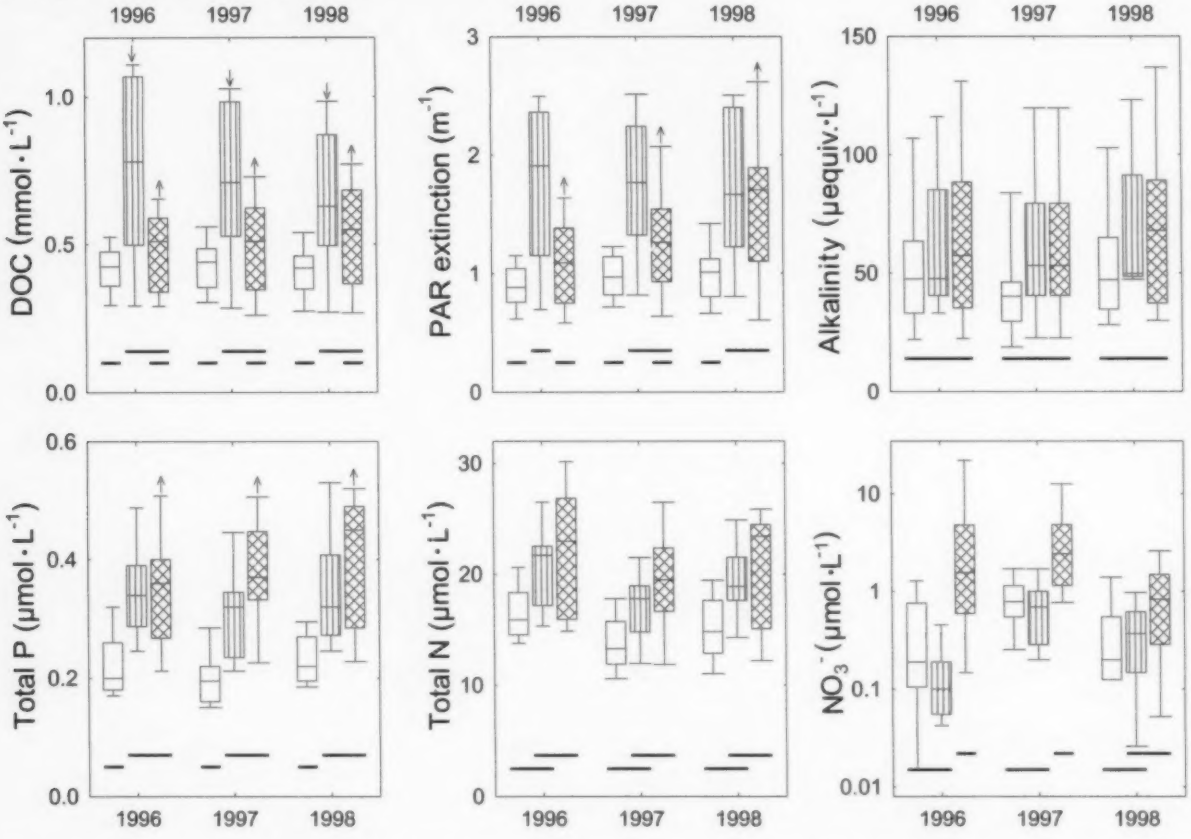
Fig. 2. Box plots showing median values with the 25th and 75th and the 5th and 95th percentiles of annual average concentrations of dissolved constituents and of the light extinction coefficient ε_{PAR} in reference (open boxes, n = 17), cut (hatched boxes, n = 7), and burnt lakes (cross-hatched boxes, n = 9). The thick horizontal lines indicate between-treatment differences: for a given year, boxes with different levels are significantly different. Arrows on top of the boxes indicate significant increasing or decreasing trends with time compared with the reference group (paired RMA). Two lakes (C40 and C44) where only a small portion of the catchment had been harvested are excluded from these analyses.



be substituted for a more easily obtained areal impact ratio (CUT/ΣLA) but with a loss of precision (models 9–11).

DOC and ε_{PAR} do not evolve at a similar rate in cut lakes. Between 1996 and 1998, DOC decreased in all cut lakes except Lake C9. Linear regression of DOC versus time (n = 9 data points) for individual lakes shows that the decrease is significant in Lakes C2 (–0.07 mmol·year^{-1}), C12 (–0.11 mmol·year^{-1}), C24 (–0.09 mmol·year^{-1}), and C29 (–0.015 mmol·year^{-1}). The decrease is also marginally significant in Lake C48 (–0.02 mmol·year^{-1}, p = 0.07). These decreases in DOC are not paralleled by decreases in ε_{PAR}. The only significant changes in ε_{PAR} were positive and occurred in Lakes C29 (+0.06 m^{-1}·year^{-1}) and C40 (+0.07 m^{-1}·year^{-1}). During the same interval, DOC changed significantly, by a much smaller amount (–0.006 mmol·year^{-1}), in only two of the 16 reference lakes.

Fire-impacted lakes differ from cut lakes in two ways in terms of DOC and ε_{PAR}. First, DOC concentrations in the fire-impacted group were not significantly different from those of reference lakes 1 year after impact (Figs. 2–4); second, they increased significantly (RMA) during the following years (Fig. 2). When individual lakes were examined by linear regression, DOC increased in all lakes except Lake FBP10, but the changes were significant only in Lakes FP2 and FP32. Likewise, ε_{PAR} was near reference levels in 1996 but increased significantly afterwards in all burnt lakes except Lakes FBP10 and FP27 (Figs. 2 and 3). By 1998, ε_{PAR} values in burnt lakes were approaching those of cut lakes. The best relationship between DOC or ε_{PAR} and watershed properties for burnt lakes included DR or VOL/WA (a surrogate for the residence time) as independent variables and explained 55–70% of the variance. By 1998, due to the increasing ε_{PAR} in burnt lakes, biological production may have been light limited in some lakes, since the midsummer epilimnion depth exceeded the compensation depth for net photosynthesis (1% incident PAR).

Several mechanisms may explain the contrasting DOC and ε_{PAR} responses of cut and burnt lakes to forest clearance. The increase in annual runoff following the loss of forest cover in Québec's boreal forest has been estimated at about 200 mm (Plamondon 1993), or 40% of the long-term runoff at our study site. In eastern Canada, this high runoff

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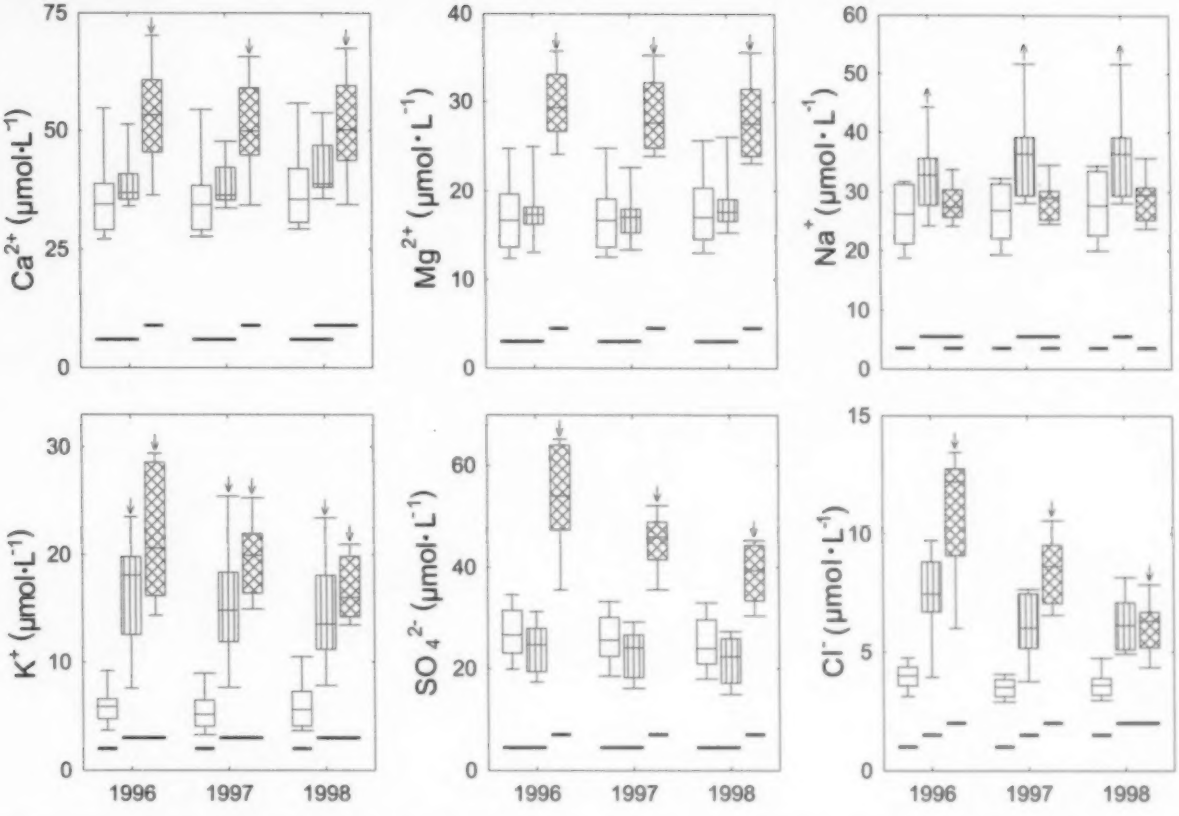
Fig. 2 (*concluded*).



is expected to persist for decades after forest clearance by harvesting or fire (Plamondon 1993). Increased runoff should increase the transfer of terrestrial DOC and colour to lakes by increasing the development of superficial flow paths through organic-rich soil layers (Mulholland et al. 1990; D'Arcy and Carignan 1997). If the transfer of terrestrial DOC and colour to lakes had been strictly caused by a rise in the water table and an increase in superficial flow path, DOC and ε_{PAR} should have been highest in burnt lakes, since their drainage areas had twice as much forest cleared as those of cut lakes. The facts do not support such a simple hydrological control of DOC and colour export to lakes affected by harvest or fire. DOC was higher in cut lakes, where runoff must have been lower than in the nearly completely deforested burnt catchments, and decreased rapidly in some of them. Moreover, DOC and ε_{PAR} were low in 1996 in burnt lakes and increased afterwards. Compared with fire, harvesting leaves large quantities of easily leached or decomposed organic material, which may have produced part of the excess DOC initially observed in cut lakes only. This fresh DOC may be less coloured than humic DOC derived from upper soil horizons, since the significant decrease in DOC seen in cut lakes during the first 3 years is not paralleled by a corresponding decrease in ε_{PAR}. We can only speculate on the reasons explaining low initial concentrations and increasing trends of DOC and colour in burnt lakes. Low export of DOC and colour from drainage areas may reflect the nearly complete loss of important organic C sources (seasonal litterfall from trees, shrubs, and herbaceous vegetation) and the partial combustion of the organic forest floor. Some DOC and colour may have been sorbed by the large quantities of charcoal left on the ground after fire (Wardle et al. 1998). The large N plus P pulse associated with fire may also have stimulated the degradation of terrestrial DOC and colour, both on land and in the water.

Phosphorus and nitrogen

TP (yearly averages) was significantly higher in cut and burnt lakes than in reference lakes (Fig. 2). A significant (RMA) seasonal pattern was observed in reference and burnt lakes but not in cut lakes (Fig. 3). Concentrations were usually at a maximum in springtime and declined by ~20% during later months in reference lakes and by ~50% in several burnt lakes. Compared with reference lakes, springtime and annual average TP concentrations in burnt lakes showed a significant (RMA) increasing trend from 1996 to 1998. In reference lakes, 52% of the variability in springtime log TP is explained by log DR and 74% by a combination of log DR and –log ΣLA (Table 2, model 12). Note, however, that an equally successful model involves log DR and –log CA ($r^2 = 0.74$). The negative influence of lake size may be interpreted as resulting from the important contribution of fringing vegetation to P loading in small lakes (Cole et al. 1990). These different models stress the point that such empirical

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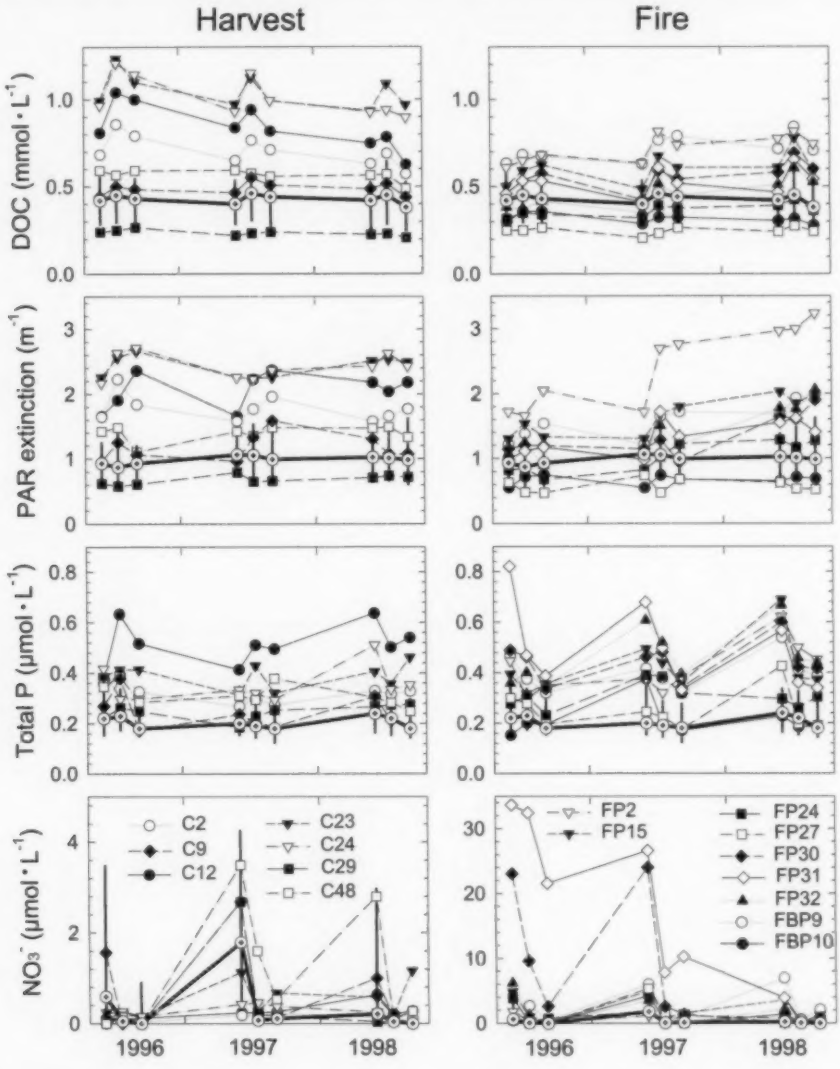
Fig. 3. Evolution of dissolved constituents and ε_{PAR} during the first 3 years following forest clearance by harvesting or fire. The thick solid lines indicate median concentrations plus and minus the 5th and 95th percentiles for reference lakes.



relationships must be interpreted with caution due to the high degree of autocorrelation between morphometric lake and watershed variables and to the large number of independent variables.

TP concentrations in several of the cut and burnt lakes were higher than the range observed in reference lakes (Fig. 3). As found for DOC and ε_{PAR}, these high TP concentrations cannot be attributed solely to the slightly higher DRs of cut and burnt lakes compared with reference lakes. As found above for DOC in cut lakes, TP was directly proportional to the DR and CUT/ΣLA (Fig. 6; Table 2, model 13, $r^2 = 0.57$) and to CUT/VOL (model 14, $r^2 = 0.70$), as found above for DOC and ε_{PAR} in cut lakes. Similar relationships are found for burnt lakes (models 15 and 16). Lake FP15 was a clear outlier in model 16, however, and was omitted from this regression. Exceptionally, a large headwater lake drains into Lake FP15 and contributes to intercept some of the P load arriving from the burnt catchment. Regression slopes and intercepts calculated separately for cut and burnt lakes are not significantly different and both groups of lakes are shown together in model 17 and Fig. 6.

Forest clearance by fire and harvesting appears to cause similar TP increases in surface waters when expressed as a function of DR and of the CUT/ΣLA (Fig. 6). The chemical form and bioavailability of P supplied from harvested and burnt drainage areas may not be identical, however. The rapid seasonal decrease in TP observed in burnt lakes is indicative of a high bioavailability compared with cut lakes, where no consistent seasonal decrease in TP occurs. Moreover, burnt lakes produced more planktonic chlorophyll *a*

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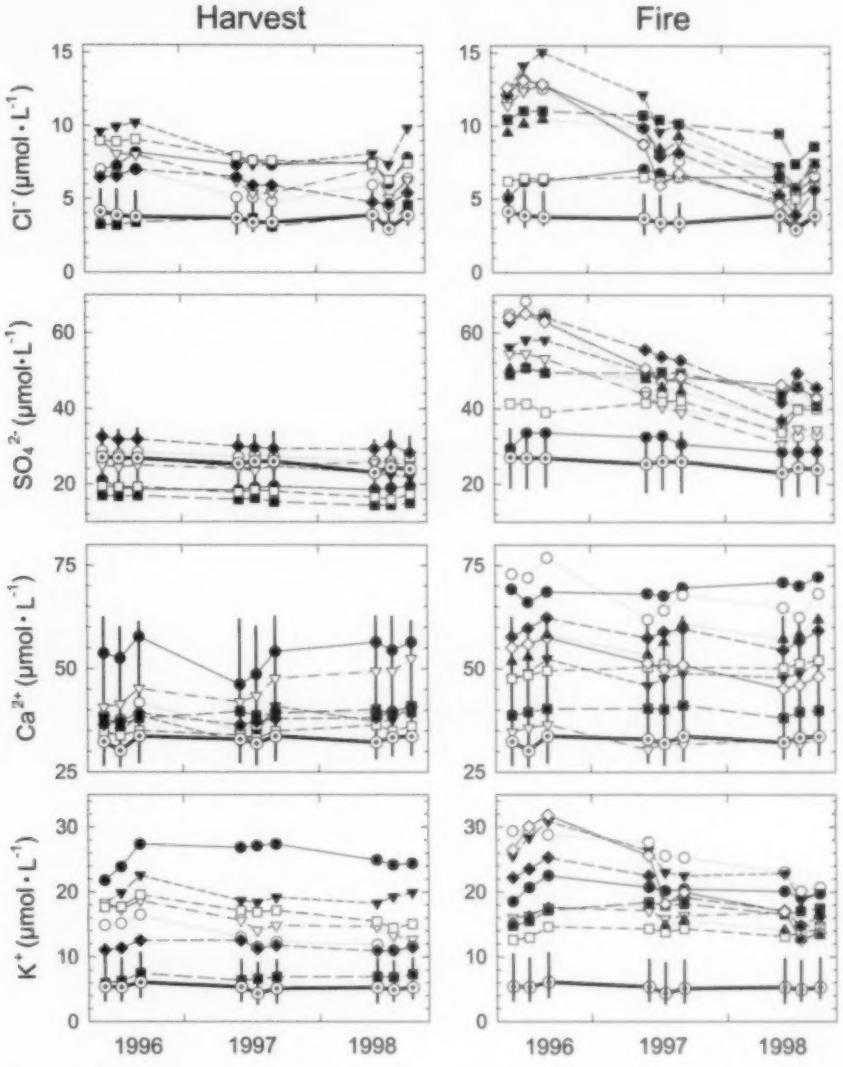
Fig. 3 (*concluded*).



per unit TP than cut lakes did (Planas et al. 2000). Springtime and mean annual TP concentrations in burnt and cut lakes may take several more years to reach background values, since they did not decrease between 1996 and 1998.

Harvesting had no significant effect on NO_3^- concentrations (RMA). In both reference and cut lakes, NO_3^- was generally low in the spring (<0.04–3 µmol·L^{-1}) and, in a majority of cases, decreased below the detection limit by midsummer (Fig. 3). Springtime NO_3^- concentrations in reference lakes were weakly but significantly related to ZM (r^2 = 0.30). Other variables expected to be related to NO_3^- (latitude, longitude, DR, residence time) played no significant role. NO_3^- concentrations were weakly but non-significantly related to indicators of acid deposition (SO_4^{2-} (positive), alkalinity (negative)). Fire had a different and more varied effect on NO_3^- concentrations (Fig. 3; note that the scales are different for cut and burnt lakes). Very high springtime concentrations (>20 µmol·L^{-1}) were measured in 1996 in two lakes (FP30 and FP31) and intermediate concentrations were observed in other lakes (FP15, FP24, and FP32), whereas NO_3^- did not exceed reference levels in some other lakes (FP2, FBP9, FBP10, and FP27). A combination of log(FIR/ΣLA) and log(catchment slope) explained 90% of the variability in springtime NO_3^- in burnt lakes (Table 2, model 18). This NO_3^- pulse was short-lived, however; by 1998, NO_3^- concentrations in all burnt lakes were near those observed in reference and cut lakes.

NH_4^+ concentrations were systematically low (<0.07–1.5 µmol·L^{-1}) and were unrelated to pH (data not shown). Although concentrations were low, median values were significantly different in burnt lakes (0.6 µmol·L^{-1}), cut lakes (0.4 µmol·L^{-1}), and reference lakes (0.3 µmol·L^{-1}). TN was

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Fig. 4. DOC versus DR for reference (○), cut (+, % harvested), and burnt lakes (●). The solid line shows the relationship between DOC and the DR for the reference lakes only (1996 values). The broken lines show the 95% confidence interval of predictions.

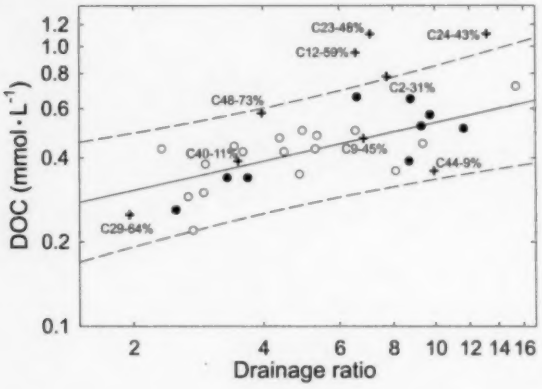
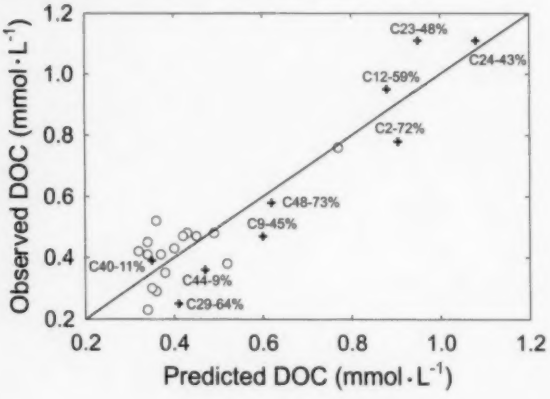
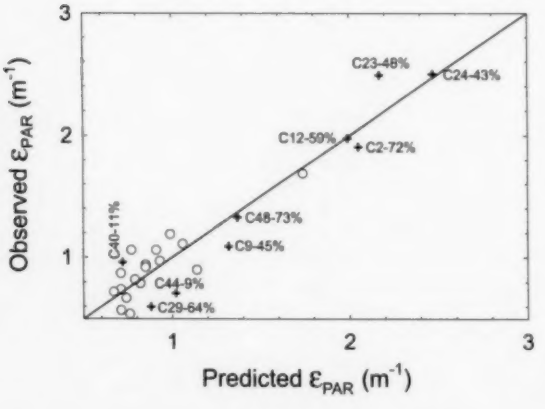


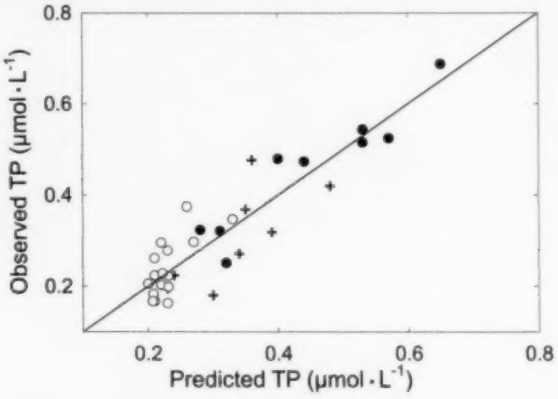
Fig. 5. Observed versus predicted DOC and light attenuation (ε_{PAR}) in reference (○) and cut lakes (+, % harvested) using volumetric impact models 3 and 6 (Table 2).





highest in burnt lakes and lowest in reference lakes (Fig. 2). Regression models for total organic nitrogen (TON = TN – (NO_3^- + NH_4^+)) for reference lakes were similar to those found for DOC, ε_{PAR}, and TP. Average TON concentrations were slightly but significantly higher in cut and burnt lakes (19.9 and 19.7 μmol·L^{-1}) than in reference lakes (15.9 μmol·L^{-1}). In cut lakes, TON was closely related to CUT:VOL, as found for DOC, ε_{PAR}, and TP (Table 2, model 19).

Fig. 6. Observed versus predicted springtime TP concentrations using the areal impact model 17 (Table 2) in reference (○), cut (+), and burnt lakes (●).



Major ions

The concentrations of several major ions (Ca^{2+}, Mg^{2+}, K^+, Cl^-) and alkalinity in reference lakes were lower in 1997 than in 1996 and 1998, likely because of a higher runoff in 1997. Annual variability in reference lakes was small for $Ca^{2+}$and Mg^{2+} (<1%), which are usually well buffered by the soil matrix, but pronounced for K^+, Cl^-, and alkalinity (9–19%). SO_4^{2-} decreased significantly (RMA) in reference lakes during the 3 years (–7%), while Na^+ increased significantly (+6%). Local variations in bedrock geology and till composition probably cause most of the spatial variability in base cations, since no significant relationships were found between cations and SO_4^{2-} concentrations in reference lakes or between cations and watershed properties, including the type and thickness of superficial deposits. A geological influence is apparent for Ca^{2+}, Mg^{2+}, and alkalinity. Six lakes (N55, N89, N122, P106, P107, FBP9) located on a particular granodioritic gneiss formation had alkalinities and Ca^{2+} and Mg^{2+} (but not Na^+ and K^+) concentrations that were up to twice as high as those of other lakes in their group.

K^+ and Cl^- concentrations were much higher in cut and burnt lakes than in reference lakes (Figs. 2 and 3) and were directly proportional to the amount of forest cleared by fire or harvest, divided by the lake's surface area or volume (Table 2, models 20–23). The different slopes of the harvest and fire models suggest that logging exports more K^+ and Cl^- than fire to surface and groundwaters. The relationships are not significantly different (analysis of covariance), however, and both perturbations may have comparable effects (Lamontagne et al. 2000). K^+ and Cl^- decreased significantly between 1996 and 1998 in cut and burnt lakes and should reach reference levels in a few more years. Cut lakes had

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Fig. 7. Evolution of DOC, TP, K^+, and ε_{PAR} in Lakes P25 (○), P106 (▲), and P110 (●) logged between 1996 and 1998 (see text for timing). The thick solid lines with dotted circles show median values plus and minus the 5th and 95th percentiles for the reference lakes.

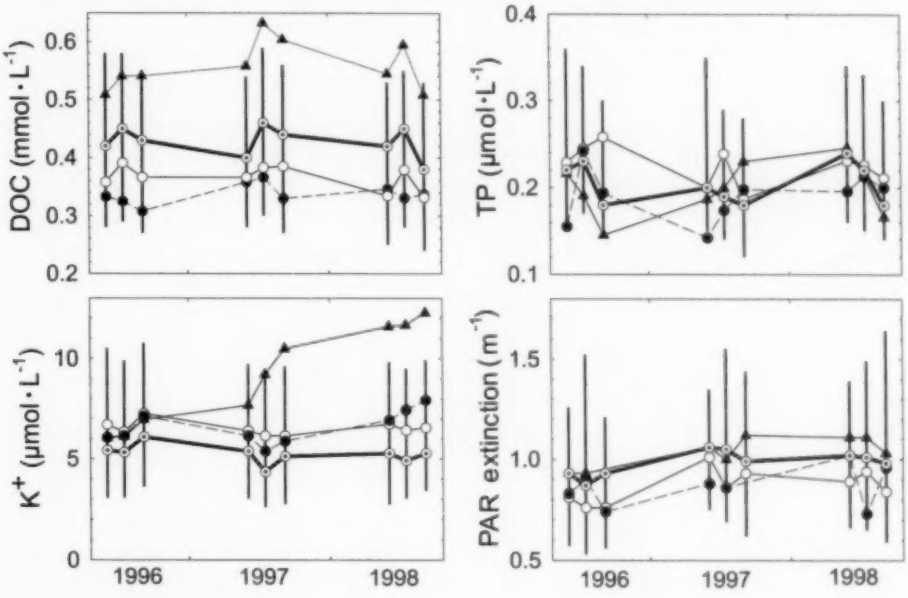

Table 3. Predicted changes in ε_{PAR}, DOC, TP, and K^+ following harvesting in lakes P25, P106, and P110.

Lake	DR	Clearcut (km^2)	Lake area (km^2)	Lake volume (m^3)	AIR ($m^2 \cdot m^{-2}$)	VIR ($m^2 \cdot m^{-3}$)	$\Delta\varepsilon_{PAR}$ (m^{-1})	ΔDOC ($mmol \cdot L^{-1}$)	ΔTP ($\mu mol \cdot L^{-1}$)	ΔK^+ ($\mu mol \cdot L^{-1}$)
P25	4.50	0.28	0.33	1.55×10^6	0.85	0.18	0.11±0.02	0.05±0.01	0.022±0.012	2.7±1.7
P106	2.97	0.32	0.41	1.89×10^6	0.78	0.16	0.10±0.02	0.04±0.01	0.020±0.011	2.5±1.5
P110	5.93	1.06	0.81	3.74×10^6	1.30	0.28	0.17±0.04	0.07±0.02	0.034±0.018	4.3±2.6

Note: The areal impact ratio (AIR) is the impacted surface area divided by the lake surface area). The volumetric impact ratio (VIR) is the impacted surface area divided by the lake volume. Expected changes in $\varepsilon subromanPAR$, DOC, TP, and K^+ are calculated from models 6, 3, 13, and 20 (Table 2).

slightly but significantly more Na^+ than reference and burnt lakes. The cause for this difference is uncertain. Important Na losses by volatilization during fire may explain lower Na^+ concentrations in burnt lakes. On the other hand, the fact that a relatively mobile ion such as Na^+ did not decrease in cut lakes between 1996 and 1998 suggests that slightly higher Na^+ concentrations in cut lakes may be due to differences in geology.

Ca^{2+} and Mg^{2+} concentrations in burnt lakes were significantly higher (two- to four-fold) than in reference and cut lakes (Figs. 2 and 3). The box plots in Fig. 2 suggest that harvesting had no significant effect on Ca^{2+} and Mg^{2+}. This conclusion should be considered with caution, as other facts point to the contrary. Although Ca^{2+} concentrations in cut lakes were within the range of concentrations observed in reference lakes, they were systematically above the median reference concentration (Fig. 3). Furthermore, lakes located on granodioritic gneiss contributed most of the variability in Ca^{2+} concentrations. When these lakes and the negligibly impacted Lakes C40 and C44 are removed from the ANOVA, the three groups of lakes become significantly different, with mean Ca^{2+} concentrations of 30.8, 39.6, and 50.7 $\mu mol \cdot L^{-1}$ in reference, cut, and burnt lakes, respectively (1996 values). Finally, Ca^{2+} (but not Mg^{2+}) is significantly related to CUT/VOL and CUT/ΣLA in cut lakes (Table 2, model 24). These observations indicate that Ca^{2+} is lost at an elevated rate, not only from burnt catchments but also from harvested ones.

Contrary to what was observed for K^+ and Cl^-, Ca^{2+} and Mg^{2+} concentrations did not change significantly with time in cut lakes compared with reference lakes. However, some individual lakes (C24, C29, C40) showed significant increases. This behaviour is expected, since divalent cations are less mobile than K^+ and Cl^- in soils and may take longer to reach surface waters. Wood contains relatively large amounts of Ca compared with other nutrients, and important quantities of Ca can be held for a few years in decaying branches and boles. Trends were more erratic in burnt lakes. As a group, and compared with reference lakes, Ca^{2+} decreased slightly but significantly with time. There were, however, significant increases in Lakes FBP10, FP27, and FP31 and significant decreases in Lakes FBP9, FP2, and FP30.

In reference lakes, SO_4^{2-} was positively related to longi-

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tude (Table 2, model 25, $r^2 = 0.52$) and negatively related to alkalinity ($r^2 = 0.33$ and 0.58 when high-alkalinity outliers N55, N89, and N122 are removed), reflecting a well-known H_2SO_4 deposition gradient in this region due to the presence of important point sources of SO_2 (Sudbury, Rouyn-Noranda) located 200–400 km to the west. A similar relationship was found for alkalinity (model 26) when high-alkalinity reference Lakes N55, N89, and N122 were removed from the data set. Note that the slope of the alkalinity model (26) is of opposite sign and twice as high as that of the SO_4^{2-} model (18). The correct acid–base stoichiometry of both relationships indicates that they are not statistical artefacts. Much higher SO_4^{2-} concentrations were observed in burnt lakes than in reference and cut lakes. High SO_4^{2-} levels in lakes draining burnt catchments were likely caused by the partial combustion of the LFH layer and B horizon, which contain 30 times more organic S than the above-ground biomass in conifer forests (Houle and Carignan 1992). In burnt lakes, SO_4^{2-} was weakly but significantly related to the impact ratio ($r^2 = 0.48$). Spatial variability in fire intensity, in humus thickness, and in the degree of humus combustion probably explains the poorer fit between SO_4^{2-} and the impact ratio.

Response of lakes harvested during the study

Four of the study lakes were logged between 1996 and 1998. Lake P106 had 24% of its catchment logged in the winter of 1996–1997, Lake P25 had 18% of its catchment logged in the summer of 1997, and Lake P110 had 22% of its catchment logged in the winter of 1997–1998. Lake P106 showed clear K^+ and Cl^- signals (Fig. 7, Cl^- not shown) arriving during the summer of 1997. In Lake P110, K^+ and Cl^- began to reach the lake during the summer of 1998, by which time they had not yet arrived in Lake P25. Lake P25 had narrow cut blocks mostly fringing the limit of its watershed. In this lake, K^+ and Cl^- liberated from branches and leaves may not have had the time to reach Lake P25 by September of 1998.

Clear-cutting had minimal effects on DOC, ε_{PAR}, and TP in these lakes (Fig. 7). Compared with median reference values, slight increases were apparent only in Lake P106 and perhaps in Lake P110. In Lake P106, after 1996, DOC and ε_{PAR} increased by about 0.05 mmol·L^{-1} and 0.2·m^{-1}, respectively, relative to median reference values. TP increased by about 0.03 μmol·L^{-1} and K^+ by 5 μmol·L^{-1}. In Lake P110, DOC and ε_{PAR} appear to have increased at most by about 0.03 mmol·L^{-1} and 0.1·m^{-1}, respectively, after 1996. Except for K^+ and Cl^-, these changes were not significant. Such limited effects are consistent with the predictions (Table 3) of the impact models proposed above (see Figs. 5 and 6 and Table 2 (models 3, 6, 13 and 20)). According to these models, in Lakes P106 and P110, DOC should not have increased by more than 0.04–0.07 mmol·L^{-1}, ε_{PAR} should not have increased by more than 0.10–0.17·m^{-1}, and TP should not have increased by more than 0.02–0.03 μmol·L^{-1}. The increase in K^+ observed in Lake P106 is also near the range predicted by model 20.

Differential effects of fire and harvest: management implications

Our observations indicate that Boreal Shield lakes respond predictably, but in some cases differently, to disturbance by fire and harvesting. Three years after impact, some responses to these disturbances appear to be similar (TP, TON, K^+, Cl^-, Ca^{2+}), while others are clearly different (DOC, ε_{PAR}, NO_3^-, SO_4^{2-}). Some effects, such as the K^+, Cl^-, NO_3^-, and SO_4^{2-} pulses that follow disturbance by fire or harvesting, are apparently short-lived, while others (DOC, ε_{PAR}, TP), which may be driven at least in part by hydrological changes, appear to evolve on a longer time scale. Some of these responses, such as the increase in DOC, ε_{PAR}, and TP in cut lakes, should be given particular attention because they appear to be long-lived and because they may adversely influence other key limnological properties. Reduced water clarity reduces mixing depth (Fee et al. 1996) and the depth of the euphotic zone, where photosynthesis can occur. In our study lakes, high DOC loads from cut lakes are associated with high methyl mercury in zooplankton and fish (Garcia and Carignan 1999, 2000). The simple impact ratio models shown above can be used, along with water quality guidelines, to define allowable cuts at the watershed scale.

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Element export in runoff from eastern Canadian Boreal Shield drainage basins following forest harvesting and wildfires

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Abstract: Element export rates from the drainage area of nine harvested, nine burnt, and 16 reference Boreal Shield lake basins in Haute-Mauricie, Québec, were estimated for the 3 years following harvesting or fires. Export rates from the drainage area of the basins were evaluated using lake sampling surveys, estimated hydrological budgets, and estimated nutrient retention during lake transit. Increases in K^+, total N, and total P export rates were similar between harvested and burnt drainage areas. However, harvested drainage areas exported more dissolved organic C, while burnt drainage areas exported more Mg^{2+}, NO_3^-, and SO_4^{2-}. Potassium cumulative losses in runoff during the 3 years of the study were of a similar magnitude as volatilization losses during fires and corresponded to ~33% of the losses by biomass removal during harvesting. While the increased export rates for N and P following fires or harvesting represented negligible losses of nutrients for the forest, they were important supplementary inputs to lakes. The differences in element export rates observed between harvested and burnt drainage areas indicate that these disturbances have different impacts on biogeochemical cycles in the Boreal Shield forest.

Résumé : Les changements dans les apports d'éléments provenant de l'aire de drainage de lacs du Bouclier Boréal de la Haute-Mauricie, Québec, ont été estimés à la suite de feux de forêt ou de l'exploitation forestière. Les taux d'exportation ont été calculés pour neuf aires de drainage "brûlés" et neuf aires de drainage "coupés" et ils ont été comparés à un ensemble de 16 aires de drainage de référence pour les 3 années post-perturbations. Les taux d'exportation ont été établis à l'aide de campagnes d'échantillonnage des lacs, d'une estimation des bilans hydrologiques et d'une estimation de la rétention des nutriments durant leur séjour dans les lacs. La hausse du taux d'exportation du K^+, du N total et du P total était similaire entre les aires de drainage brûlées et coupées. Cependant, le taux d'exportation du C organique dissous était plus élevé dans les aires de drainage coupées et ceux du Mg^{2+}, du NO_3^- et du SO_4^{2-} plus élevés dans les aires de drainage brûlées. Pour les 3 années de l'étude, la perte cumulative de K^+ par le ruissellement était du même ordre de grandeur que celle par volatilisation durant les feux et correspondait à ~33% du K^+ perdu par prélèvement de la biomasse durant l'exploitation forestière. Le taux d'exportation accrû de N et de P à la suite des perturbations était une perte de nutriments négligeable pour la forêt mais représentait un apport supplémentaire important pour les lacs. Les différences observées dans le taux d'exportation de certains éléments démontrent que l'exploitation forestière et les feux affectent les cycles biogéochimiques différemment dans la forêt du Bouclier Boréal.

Introduction

Forest harvesting and forest fires are important disturbances in the Boreal Shield forest in eastern Canada (Natural Resources Canada 1996). Annually, in the Province of Québec, ~1% of the boreal forest is harvested and <0.1 to 0.4% is affected by forest fires (Ministère des Ressources naturelles 1996). Some current forest harvesting management initiatives seek to emulate the effect of natural disturbances during forestry operations. However, the similarity of wildfires and harvesting on element loss from drainage areas (drainage area = terrestrial part; basin area = drainage area + lake area) and their relative impacts on downstream freshwater ecosystems are not well known. Biogeochemical cy-

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cles are affected differently by forest fires and tree harvesting. Although forest fires and harvesting both result in increased runoff from reduced evapotranspiration (Verry 1986; Bayley et al. 1992), forest fires tend to mineralize the organic soil (MacLean et al. 1983), while this layer is better preserved following harvesting. Whether the organic soil will be preserved following a disturbance will have important implications for soil mineralization and plant colonization processes, which are important controls on nutrient losses in runoff (Vitousek 1981).

In Shield conifer forests, losses of base cations (K^+, Ca^{2+}, and Mg^{2+}), NO_3^-, and total P (TP) above background rates may last for 5–9 years following wildfires (Wright 1976; Bayley and Schindler 1991). A similar effect is usually observed following harvesting (Nicolson et al. 1982; Plamondon et al. 1982). In some unproductive forests, however, the export of nutrients is occasionally unaffected by harvesting (Vitousek 1981). Increased export of dissolved organic C (DOC) is suspected to be important in harvested Shield basins (Krause 1982) but has not been well characterized. Changes in DOC inputs have been shown to have important implications for the physical, chemical, and biological properties of Shield lakes (Schindler et al. 1992, 1997).

We studied the response of 16 reference and 18 impacted Shield lake basins in Haute-Mauricie, Québec, from 1996 to 1998. The drainage area of nine basins had been commercially harvested and nine others had sustained forest fires in 1995. We estimated element export rates from the drainage area of the basins using time series of element concentration from lakes. Our objectives were twofold: first, we compared element loss rates from harvested and burnt drainage areas relative to reference drainage areas, and second, we evaluated whether the cumulative export of nutrients in runoff in perturbed basins during the study was a significant loss relative to element volatilization during fires or biomass removal during harvesting.

Methods

The study area (~50 000 km^2) is centered on Gouin Reservoir, Québec (48°50′N, 75°00′W), at the transition of the boreal mixed and boreal conifer forest (see detailed map and description in Carignan et al. 2000). The landscape is typical of the Canadian Shield, with a low relief, thin surface deposits, and numerous lakes and wetlands. Extensive forestry operations are ongoing throughout the study area, where three large wildfires (30 000 – 50 000 ha involving over 1000 lakes) occurred during the summer of 1995. This provided a unique opportunity to simultaneously compare the effect of both disturbances on similar lakes. Thirty-eight lake basins were selected on the basis of the following criteria: forest age >50 years, wetlands <6% of the drainage area, drainage ratio 2 to 15, hydrological order 1, fetch >1 km, fire intensity medium to severe (no salvage logging), and maximum depth >5 m.

Four of the original 20 reference basins (drainage areas undisturbed for the last 75 years) were excluded from the analysis because they were subsequently harvested in 1997 or 1998 (Carignan et al. 2000). In the remaining lakes, lake order is not always exactly 1 because 14 lakes have smaller lakes in their drainage. With the exception of one basin (FP15), these smaller lakes represent, on average, only 16% of the surface area of the downstream study lakes (Table 1). Nine basins had 50–100% (average = 90%) of their drainage area severely burnt and nine other basins had 8.5–73% (average = 47%) of their drainage area harvested in 1995. Forest harvesting was usually in the form of 200- to 300-ha cuts with protection of regeneration and soils, with 20-m buffer strips fringing streams, lakes, and wetlands (Éditeur officiel du Québec 1996). The principal species harvested were black spruce (*Picea mariana* (Mill.) B.S.P.) and white birch (*Betula papyrifera* Marsh.). Vegetation was usually lost up to the shoreline in burnt basins.

Lake sampling

Duplicate integrated water samples of the euphotic zone (i.e., depth of 1% light penetration, usually 2–5 m) were collected three times per year at or near maximum lake depth. Lakes were sampled in spring within 2 weeks of ice-out (late May to early June), midsummer (July), and early fall (late August to mid-September). Samples were filtered within 12 h when necessary (Gelman 0.45-μm filter membrane), stored at 4°C, and usually analyzed within 48 h using standard methods (Carignan et al. 2000). Measured properties included DOC, TP, total N (TN), NO_3^-, NH_4^+, major ions (Ca^{2+}, Mg^{2+}, Na^+, K^+, SO_4^{2-}, and Cl^-), pH, and alkalinity.

Estimation of drainage area element export rates

Drainage area element export rates (D, moles or equivalents per hectare per year) were estimated by back-calculation (see below) using the time series of element concentration from the lakes. The first step involved in back-calculation was to estimate runoff from the lake basins. The lake basins are remote and could not be gauged with traditional hydrological techniques. Runoff from each lake basin was estimated using three gauged river basins with natural flow regimes in the study area (the Gatineau, Bell, and Chamouchouane rivers) (Table 2). Three time intervals were defined, corresponding to the midpoint in time between lake sampling surveys (spring (1 January to 15 June), summer (15 June to 15 August), and fall (15 August to 31 December)). For each lake basin, runoff (r) for a given time interval was the mean from the reference river basins weighted as a function of the distance between the lake basin and the geographical center of the reference river basins:

$$(1) \qquad r_{i,j,k} = \frac{\sum_{x=1}^{3}\left(\frac{1}{d_{i,x}^2} r_{j,k,x}\right)}{\sum_{x=1}^{3}\frac{1}{d_{i,x}^2}}$$

where $r_{i,j,k}$ is runoff from the ith lake basin for the jth year and kth sampling interval, $r_{j,k,x}$ is runoff from the xth reference river basin for given period, and $d_{i,x}$ is the distance between the ith lake basin and the xth reference river basin.

The reference river basins are much larger (6840 – 22 200 km^2) than the study lake basins (0.6–2.2 km^2), giving the possibility of differences in the magnitude and timing of runoff between basin types. Biases in the timing of runoff will be minimized by hydrological budgets being compiled on a seasonal basis. Biases in magnitude of runoff would affect our exports rates on a quantitative but not on a qualitative basis because the bias would apply to both disturbed and reference study basins. There are no gauged small basins within several hundred kilometres of the study area.

Impact of harvesting and fires on runoff

Forest harvesting and forest fires usually increase runoff from small Precambrian Shield basins (Verry 1986; Plamondon 1993). In general, runoff is more strongly affected when evapotranspiration is an important component of the hydrological budget. In Haute-Mauricie, evapotranspiration (~475 mm) is an important proportion of precipitation inputs (~1000 mm), and tree removal by harvesting or fires should yield an important increase in yearly runoff. Plamondon (1993) estimated that the potential for

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Table 1. Morphometry (mean and range) of 34 harvested, burnt, and reference basins in Haute-Mauricie.

	Harvested	Burnt	Reference
LA (km^2)	0.56 (0.18–2.3)	0.40 (0.17–0.64)	0.43 (0.15–0.80)
DA (km^2)	3.4 (0.59–10)	4.9 (0.57–20)[a]	2.0 (0.45–4.5)
DA:LA	7.2 (2.0–14)	12 (2.5–41)[a]	5.4 (2.3–15)
LA_{un}:LA[b]	0.15 (0.08–0.31)	0.85 (0.14–3.2)[a]	0.13 (0.01–0.11)
Z_{max} (m)	14 (5–30)	17 (10–34)	12 (7–21)
Z_m (m)	4.3 (2.1–7.5)	5.8 (4.2–10)	4.3 (2.1–8.5)
% DA cut or burnt	47 (8.5–73)	91 (50–100)	0 (0–1)
n	9 (4)	9 (5)	16 (5)

Note: LA, lake area; DA, drainage area; DA:LA, drainage ratio (excluding upstream lakes); LA_{up}:LA, ratio of upstream lake area to lake area; Z_{max}, maximum depth; Z_m, mean depth; *n*, number of lakes in each group (number of basins containing upstream lakes in parentheses). Additional information about the study basins can be found in Carignan et al. (2000).

[a]Without Lake FP15: mean DA = 3.1 km^2, mean DA:LA = 7.9, and mean LA_{up}:LA = 0.27.

[b]For basins with $LA_{up} \neq 0$ only.

Table 2. Characteristics of the reference river basins used to estimate runoff from the study lake basins.

	Bell	Gatineau	Chamouchouane
Location	76°38′N, 48°41′W	75°17′N, 47°44′W	73°27′N, 49°24′W
Environment Canada gauging station No.	03AC004	02LG005	02RF001
Basin area (km^2)	22 200	6840	15 300
1996 runoff (mm)	533	544	609
1997 runoff (mm)	641	692	750
1998 runoff (mm)	463	460	546
Long-term mean runoff (mm)	555	582	623

Note: All reference river basins have natural flow regimes. Coordinates are for the geographical center of the river basins (not the gauging station locations). Daily runoff from 1996 to 1998 obtained from Direction du milieu hydrique, Ministère de l'Environnement et de la Faune, 2360, chemin Sainte-Foy, Sainte-Foy, QC G1V 4H2, Canada.

Table 3. Location of four precipitation monitoring stations bounding the Haute-Mauricie region, with the wet-only deposition (equiv.·ha^{-1}·$year^{-1}$) of selected elements.

	La Morandière	Lebel-sur-Quevillon	Parent S	Pémonca
Environment Canada Station No.	7094026	7094275	7075799	7065900
Location	77°37′N, 48°37′W	76°58′N, 49°03′W	74°37′N, 47°55′W	72°42′N, 48°45′W
SO_4^{2-}	325	269	262	174
NO_3^-	174	134	140	123
Ca^{2+}	55	50	35	45
H^+	310	220	260	250
Cl^-	14	23	17	23

Note: Monthly deposition for 1990–1996 obtained from Direction du milieu atmosphérique, Ministère de l'Environnement et de la Faune, 675, boul. René-Lévesque est, 5ième étage, Québec, QC G1R 5V7, Canada.

an increase in runoff was 200 mm following harvesting in this region (i.e., a 38% increase of total yearly runoff). We used Plamondon's (1993) estimate as the increase in runoff from drainage areas following 100% tree removal. In each disturbed drainage area, the increase in runoff was proportional to the area burnt or harvested (i.e., a 2-mm increase in runoff for each percentage of the drainage area burnt or harvested). The increase in runoff was equally distributed between the three yearly sampling intervals.

Wet deposition to lake surfaces

Direct deposition to lake surfaces is an important component of lake nutrient budgets and was estimated in a manner similar to lake basin runoff. The Quebec Ministry of the Environment maintains a network of wet-only deposition chemistry stations throughout the province (Jacques and Boulet 1988). Four stations bounding the study area were used to estimate direct precipitation inputs to lake surfaces (Table 3). Atmospheric deposition (*P*, moles or equivalents per hectare per year) to the surface of each lake was determined using the same weighting procedure as the one used for estimating runoff (but with four reference stations instead of three reference river basins). A gradient of SO_4^{2-} deposition occurs from the west to the east of the study area, in part because of the occurrence of smelters ~300 km to the west, in the Abitibi region. The provincial network measures the input of H^+, major cations, Cl^-, SO_4^{2-}, NH_4^+, and NO_3^-. TP, DOC, and TN inputs were estimated from the literature (Table 4). Precipitation chemistry data were available only for the first year of the study (1996); the average deposition from 1990 to 1996 was used for the 1997–1998 budgets.

Back-calculation of D from a lake mass-balance model

The general element mass-balance for the lakes was defined as

$$(2) \qquad \frac{d[x]}{dt} = (J_D + J_P - J_o - S) / V$$

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Table 4. Atmospheric deposition rates (P, mol·ha^{-1}·year^{-1}) and mass-transfer coefficients (v, m·year^{-1}) estimated from the literature.

Variable	Range of literature values	Value used in this study
P_{TP}	2.9–13	6
P_{TN}	400–1143	400
P_{DOC}	725–2300	1000
$v_{SO_4^{2-}}$	0.40–0.54	0.40
$v_{NO_3^-}$	2.4–12.5	7.4
v_{TP}	4.7–13.7	7.9
v_{DOC}	2.3–4.1	2.3

where $d[x]/dt$ is the change in lake water concentration of chemical species x over time (moles per cubic metre per year), J_D is the load from the drainage area (moles per year), J_P is the load from atmospheric deposition to the lake surface, J_o is the loss via outflow, S is the apparent sedimentation loss (moles per year), and V is the lake volume (cubic metres). Rearranging and setting eq. 2 as a finite difference equation gives

$$(3) \qquad V\Delta[x] = J_D + J_P - J_o - S$$

where $\Delta[x]$ is the fall concentration of x minus the fall concentration of x in the previous year. Thus, $V\Delta[x]$ (or ΔM) is the change in the mass of x in the lake for a given year (moles or equivalents per year). Concentration data were not available for 1995. We first assumed that fall concentrations in 1995 and 1996 were similar in reference lakes. This approximation is reasonable because only small changes in element concentration were observed in the reference lakes between 1996 and 1998 (Carignan et al. 2000). Two approaches were taken to estimate ΔM in 1996 in harvested and burnt basins. First, empirical models relating basin morphometry, latitude, and longitude to fall element concentrations were evaluated for the reference lakes. For the chemical species with a strong correlation with basin location or morphometry (SO_4^{2-}, TP, and DOC), models were used to estimate preimpact fall concentrations in 1995 in the harvested and burnt basins (S. Lamontagne and R. Carignan, unpublished data). For the other species (Ca^{2+}, Mg^{2+}, Na^+, K^+, NO_3^-, Cl^-, and TN), fall 1995 concentrations were approximated as the average fall concentration in 1996 in reference lakes.

We assumed that outflow concentrations equaled euphotic zone concentrations and calculated the annual loss of dissolved species at the outflow as

$$(4) \qquad J_o = \sum_{t=1}^{3} \{(r_t \mathrm{LA} + r_t \mathrm{DA} + r_t \mathrm{DA}f/E)[x]_t\}$$

where r_t is the runoff estimated for a given sampling interval (metres),LA is lake area, DA is drainage area, f is the proportion of the drainage area cut or burnt, E is the coefficient of increase in runoff following harvesting or fire (0.0666 m·sampling interval^{-1} or 0.2 m·year^{-1}), and $[x]_t$ is the euphotic zone element concentration for a given sampling interval.

To estimate sedimentation losses (S), chemical species were classed into "conservative" (Ca^{2+}, Mg^{2+}, Na^+, K^+, and Cl^-) and "nonconservative" (NO_3^-, SO_4^{2-}, DOC, TP, and TN) groups based on their expected in-lake behavior. For nonconservative chemical species, it was assumed that some retention occurred during lake transit. A search of the literature was made to obtain representative mass-transfer coefficients (v, metres per year) in Shield lakes for each species (Table 4). Mass transfer coefficients are usually determined empirically from mass-balance budgets and can be visualized as a net yearly flux from the water column to the sediments proportional to the mass of a given solute contained in v metres of the water column. This is an apparent sedimentation rate because losses through other processes (phytoplankton uptake, transformation to other forms, etc.) are also included but do not necessarily involve "sedimentation" to the lake bottom. For conservative chemical species, S always equaled zero. For nonconservative species (Reckow and Chapra 1983):

$$(5) \qquad S = \mathrm{LA}v[\bar{x}]$$

where $[\bar{x}]$ is the average euphotic zone concentration of a given chemical species during a given year.

Setting J_D as D·DA and, similarly, J_P as P·LA and rearranging eq. 3 to solve for D gives

$$(6) \qquad D = \frac{\Delta M + J_o + S - P \cdot \mathrm{LA}}{\mathrm{DA}}$$

In basins containing upstream lakes, however, eq. 6 will tend to overestimate D if direct element deposition to upstream lakes is an important part of budgets or will underestimate D if sedimentation loss in upstream lakes is important. Thus, for basins containing upstream lakes, a modification of eq. 6 was used to include direct atmospheric deposition to, and element retention within, upstream lakes. In a first step, the DA of each basin was separated into a direct drainage area (DDA) and upstream lake subbasins. In a second step, retention (R, (mass in – mass out)/mass in) in upstream lakes had to be evaluated with a model that did not require that element concentrations in the lakes were known. With a steady-state approximation (i.e., by assuming $\Delta M \sim 0$ in upstream lakes), the proportion of the load from precipitation and the drainage area that was retained in upstream lakes could be evaluated from the hydrological properties of the subbasins using (Rechow and Chapra 1983):

$$(7) \qquad R = \frac{v}{v + q_s}$$

where q_s is the areal water discharge (r(LA + DA)/LA) for a given upstream lake subbasin. Assuming that D is constant in the DDA and in the DA of each subbasin, for the case with k subbasins, eq. 6 modifies to

$$(8) \qquad D = \frac{\Delta M + J_o + S - P\left\{\sum_{k=1}^{n}\left[\mathrm{LA}_k(1 - R_k)\right] + \mathrm{LA}\right\}}{\sum_{k=1}^{n}\left[\mathrm{DA}_k(1 - R_k)\right] + \mathrm{DDA}}$$

where LA is the lake area of the study lake, LA_k is the lake area in subbasin k, DA_k is the drainage area of subbasin k, and R_k is the retention coefficient of the lake in subbasin k.

Although eq. 8 appears to be a drastic modification to eq. 6, with the exception of the Lake FP15 basin, the D estimates obtained with either equation were similar. Using eq. 8 and excluding Lake FP15, the average D for lake basins containing upstream lakes was higher by 1% for SO_4^{2-}, 5% for DOC, 9% for NO_3^-, 13% for TN, and 13% for TP than when using eq. 6. For Lake FP15 only, D was higher by 3, 18, 112, 28, and 62% for the same chemical species, respectively, when using eq. 8. Although using a steady-state model to estimate R may not be accurate for the disturbed basins, with the exception of Lake FP15, the potential for direct precipitation inputs and retention within upstream lakes is small.

Estimation of flux per unit of disturbed drainage area

Drainage areas were impacted to various degrees by harvesting or fires (Table 1). To compare impacts between basins, element ex-

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port rates standardized by disturbed drainage area (D_d) were estimated using

$$(9) \quad D = F_d D_d + F_u D_u$$

where F_d and F_u are the proportion of the drainage area that is disturbed and undisturbed, respectively, and D_u is the drainage area element export rate expected under undisturbed conditions. Rearranging eq. 9 yields

$$(10) \quad D_d = \frac{D - F_u D_u}{F_d}$$

The D_u was approximated as the average D in the reference basins during a given year. Because estimates of D_d could have a large error when F_d is low, D_d for Lakes C40 and C44 (which only had 8.5 and 10% of their drainage area harvested, respectively) was not estimated.

The statistical significance for the difference in D_d between harvested and burnt basins was evaluated using t tests. Because there was a limited overlap in the proportion of the drainage areas impacted by each type of disturbance, the tests were only aimed at determining the likelihood that the observed differences were due to chance (i.e., not to "prove" in a statistical sense that Shield basins respond differently to fire or harvesting). The statistical comparison between D_d from impacted basins and D from reference basins was more complex because the average D from reference basins is already used to estimate D_d. For this later comparison, the statistical significance for the difference in fluxes was evaluated using a permutation test (Legendre and Legendre 1998). For each trial (10 000 in total), reference basins were randomly split into two groups. The mean D in one subset of reference basins was used to estimate D_d in disturbed basins. The second subset of reference basins was used in a permutation test, which yields a result similar to that of a t test (Legendre and Legendre 1998).

Scenarios of element loss from drainage areas

Increased runoff following tree removal and sedimentation losses in lakes were expected to be important factors when determining element export rates from drainage areas (eqs. 4 and 5). However, runoff and element retention in lakes could only be approximated with our study design. Therefore, we estimated D and D_d using four scenarios of catchment runoff and element retention in lakes: (*i*) no increase in runoff occurred following fires or harvesting and no retention in lakes, (*ii*) only an increase in runoff occurred, (*iii*) only retention in lakes occurred, and (*iv*) both an increase in runoff and retention in lakes occurred. The aim in comparing these scenarios was to determine to what extent the inferred patterns in element export rates were affected by two of the most important assumptions used in the model.

Results

Harvesting and fires generally increased element export rates from harvested and burnt drainage areas relative to reference drainage areas (Fig. 1). In harvested basins, the magnitude of the increase in D was positively related to the percent drainage area cut for Ca^{2+}, Mg^{2+}, Na^+, K^+, Cl^-, and TP (Fig. 1). In burnt basins, relationships between the percent drainage area disturbed and D could not be tested because most drainage areas were nearly completely burnt (Fig. 1). With the exception of TN and one outlier for Cl^-, export rates from reference drainage areas had a smaller range than those in disturbed drainage areas.

When element export rates were standardized by D_d, some similarities and contrasts were found between harvested and burnt drainage areas (Fig. 2). In general, D_d values were similar between burnt and harvested drainage areas for K^+ (threefold to eightfold reference), TN (twofold to threefold reference), and TP (twofold reference). However, D_d in burnt drainage areas was higher for Mg^{2+} (twofold to threefold reference), SO_4^{2-} (threefold to fourfold reference), and NO_3^- (up to 17-fold reference). The D_d in harvested drainage areas was higher for DOC (twofold to threefold reference) in 1996 and 1997. The D_d for Cl^- was initially highest in burnt drainage areas but decreased below rates in harvested drainage areas by 1998.

The D_d values from harvested and burnt drainage areas were highest for most elements in 1996 and tended to decline in 1997 and 1998 (Fig. 2). Noticeable departures from this trend were small peaks in NO_3^- export from harvested areas and in Na^+ and DOC exports from burnt areas in 1997. The export of divalent cations, Na^+, SO_4^{2-}, NO_3^-, and DOC from reference drainage areas was also highest in 1997, the year with the highest runoff (Table 2). In 1998, 3 years after fires or harvesting had occurred, export rates from harvested and burnt drainage areas tended to still be above rates in reference drainage areas.

Cumulative exports with different mass-balance scenarios

Comparison of cumulative exports (as D_d) estimated from the four mass-balance scenarios revealed that the main patterns in element export following harvesting or fires were independent of two of the most important assumptions used in the model (Table 5). The differences in cumulative element exports between scenarios were largest for chemical species with high mass-transfer coefficients (DOC, TP, and NO_3^-) and smallest for conservative chemical species. The cumulative export of conservative chemical species was higher by 17–30% in scenarios including an increase in runoff following disturbance. For chemical species with high mass-transfer coefficients, the range in exports between scenarios could vary from 50% to severalfold. However, for all scenarios, cumulative exports from burnt drainage areas for Ca^{2+}, Mg^{2+}, K^+, SO_4^{2-}, NO_3^-, Cl^-, TP, and TN were 1.5-fold to severalfold higher than in reference basins. Similarly, for all scenarios, cumulative exports from harvested areas for Na^+, K^+, Cl^-, TP, TN, and DOC were 1.5-fold to severalfold higher than in reference areas. For all scenarios considered, the main difference between harvested and burnt drainage areas was higher DOC exports in harvested basins. Thus, while the magnitude of exports was dependent on the parameters used in the model, the patterns between harvested, burnt, and reference basins remained similar.

Uncertainty on TP flux estimates

Despite a relatively small error on average fluxes (Fig. 2), TP export estimates are the most uncertain because both precipitation input to lake surfaces and sedimentation losses were important components of the budgets (Table 6). Both the atmospheric deposition of TP per unit lake surface (P_{TP}) and the TP mass-transfer coefficient (v_{TP}) were taken from the literature and may be biased estimates for our lake population. A sensitivity analysis was made to determine the influence of variation in P_{TP} and v_{TP} on TP flux estimates. The

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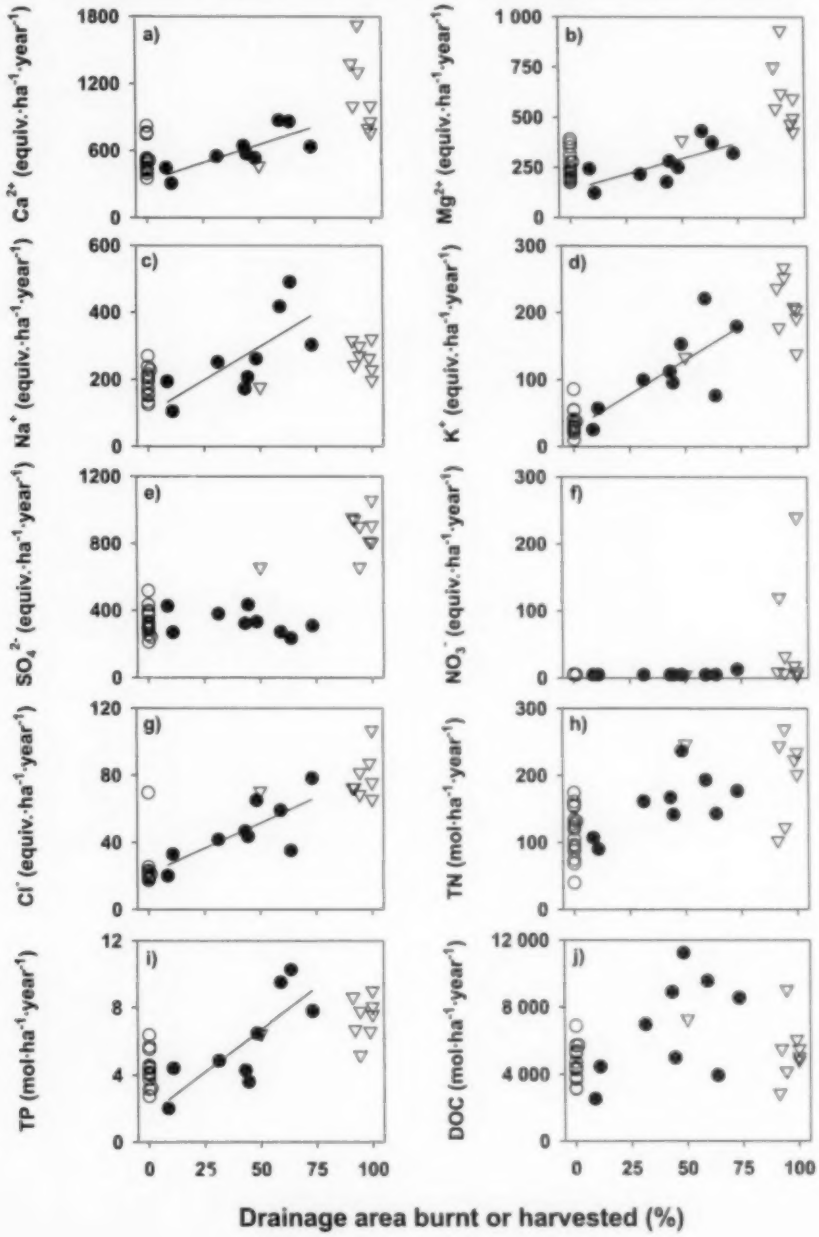
Fig. 1. Element export rates from harvested (solid circles), burnt (triangles), and reference drainage areas (open circles) in Haute-Mauricie (mean rates for the 3 years following fires or harvesting). Least-squares linear regressions between element export rates and the percentage of drainage area disturbed were evaluated for the harvested basins (results in parentheses in the following). (*a*) Ca^{2+} ($P = 0.01$, $r = 0.80$); (*b*) Mg^{2+} ($P = 0.03$, $r = 0.73$); (*c*) Na^{+} ($P = 0.03$, $r = 0.73$); (*d*) K^{+} ($P = 0.02$, $r = 0.74$); (*e*) SO_4^{2-} (not significant); (*f*) NO_3^{-} (not significant); (*g*) Cl^{-} ($P = 0.02$, $r = 0.76$); (*h*) TN (not significant); (*i*) TP ($P = 0.01$, $r = 0.80$); (*j*) DOC (not significant).



range for natural variability in both parameters was estimated as ±50% (Table 4). In addition to the sensitivity analysis, D for TP (D_{TP}) was also estimated using Prairie's (1989) model. Prairie's (1989) model assumes that net TP sedimentation is a function of both the load and the lake content of TP (instead of just the lake content in eq. 6). This approach appears to be conceptually more sound for this element (Prairie 1989).

Variability in v_{TP} and P_{TP} substantially affected the magnitude of the estimated TP export rates from harvested,

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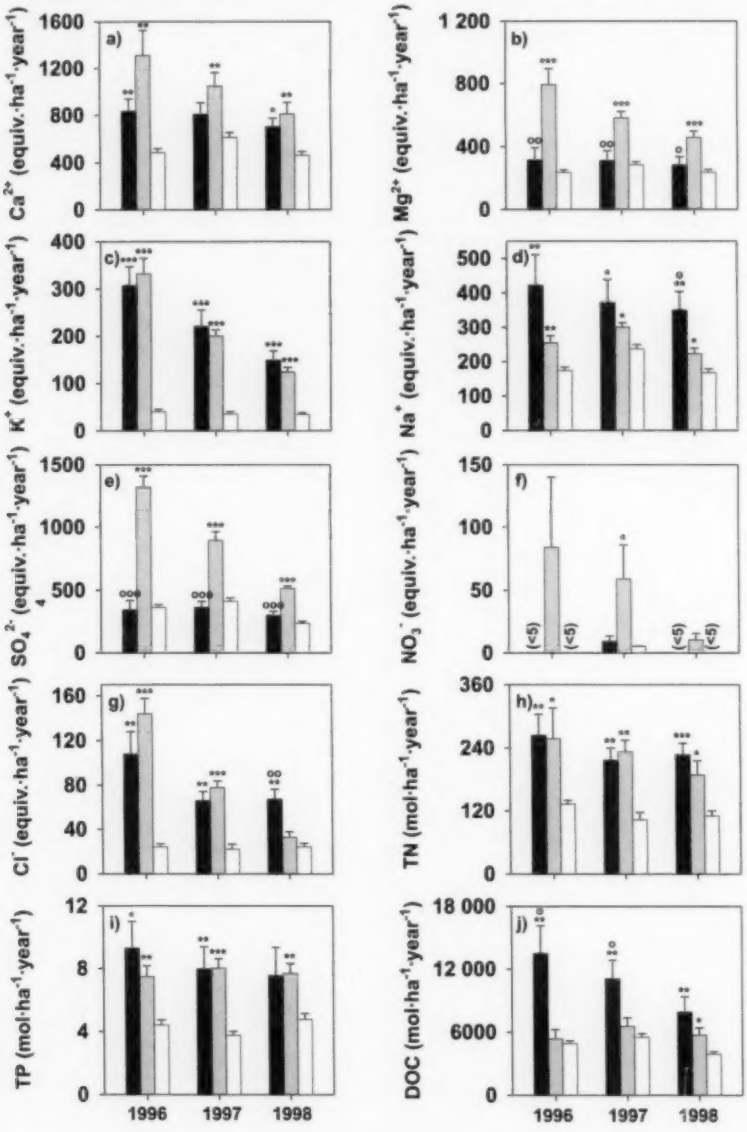
Fig. 2. Annual export rates from harvested (solid bars) and burnt (gray bars) drainage areas corrected for the percentage of the drainage area disturbed. Statistical significance tests between disturbed and reference drainage areas (white bars) are expressed with asterisks and between harvested and burnt drainage areas are expressed with circles. Single symbol = $P < 0.05$; double symbol = $P < 0.01$; triple symbol = $P < 0.001$. Error bars represent 1 SE.



burnt, and reference drainage areas (S. Lamontagne, unpublished data). The mean D_{TP} for reference drainage areas was the most sensitive to variability in P_{TP} and v_{TP} (range = 1.2–8.0 mol·ha^{-1}·year^{-1} or 3.7–25 mg·m^{-2}·year^{-1}). The discrepancy between Prairie's (1989) and our model was also largest in reference basins, where the average D_{TP} ranged from 3.8 to 4.8 mol·ha^{-1}·year^{-1} (12–15 mg·m^{-2}·year^{-1}) with our model (using v_{TP} = 7.9 and P_{TP} = 6) and from 1.2 to 1.5 mol·ha^{-1}·year^{-1} (3.7–4.7 mg·m^{-2}·year^{-1}) with Prairie's (1989) model. Although the magnitude of D_{TP} varied substantially using different models, or sets of parameters, the tendency for D_{TP} in harvested and burnt drainage areas to be larger than in reference drainage areas was always maintained.

Discussion

Forest harvesting and forest fires result in increased element export rates from drainage areas to lakes in Haute-

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Table 5. Cumulative exports from 1996 to 1998 from harvested and burnt drainage areas (as D_d) and from reference drainage areas in Haute-Mauricie according to four mass-balance models: *(i)* no sedimentation losses and no increased runoff in disturbed areas, *(ii)* with increased runoff, *(iii)* with sedimentation losses, and *(iv)* with both increased runoff and sedimentation losses.

Model	Ca^{2+} (equiv.·ha^{-1})	Mg^{2+} (equiv.·ha^{-1})	Na^{+} (equiv.·ha^{-1})	K^{+} (equiv.·ha^{-1})	SO_4^{2-} (equiv.·ha^{-1})	NO_3^{-} (equiv.·ha^{-1})	Cl^{-} (equiv.·ha^{-1})	TP (mol·ha^{-1})	TN (mol·ha^{-1})	DOC (mol·ha^{-1})
Harvested										
1 ($v = 0$, $E = 0$)	1900	700	940	580	710	<15	200	7.7	360	20 000
2 ($v = 0$, $E \neq 0$)	2300	910	1100	680	990	<15	240	9.6	460	25 000
3 ($v \neq 0$, $E = 0$)	1900	700	940	580	710	<20	200	23	590	28 000
4 ($v \neq 0$, $E \neq 0$)	2300	910	1100	680	990	<20	240	25	710	32 000
Burnt										
1 ($v = 0$, $E = 0$)	2500	1500	610	540	2000	75	210	6.8	330	9 700
2 ($v = 0$, $E \neq 0$)	3200	1800	780	660	2600	91	260	9.0	450	13 000
3 ($v \neq 0$, $E = 0$)	2500	1500	610	540	2200	136	210	21	580	15 000
4 ($v \neq 0$, $E \neq 0$)	3200	1800	780	660	2700	154	260	23	710	18 000
Reference										
1 ($v = 0$, $E = 0$)	1600	760	580	110	870	<15	71	1.4	79	7 700
3 ($v \neq 0$, $E = 0$)	1600	760	580	110	1010	<15	71	13	350	14 000

Table 6. Mean values for the different components of the element mass-balance for harvested, burnt, and reference basins for TP in 1996 (using scenario *iv*).

	Harvested ($n = 9$)	Burnt ($n = 9$)	Reference ($n = 16$)
$+J_o$/DA	2.4	3.4	1.7
$-J_p$/DA	1.2	1.1	1.5
$+S$/DA	4.6	4.1	4.2
$+\Delta M$/DA	0.61	0.70	0[a]
D	6.4	7.1	4.4

Note: All rates standardized as mol·ha drainage area^{-1}·year^{-1}.
[a]By definition in reference basins for 1996.

Table 7. Cumulative cation and anion flux (equiv.·ha^{-1})between 1996 and 1998 in harvested (as D_d), burnt (as D_d), and reference drainage areas in Haute-Mauricie.

	Harvested	Burnt	Reference
Cations			
Ca^{2}+	2300	3200	1600
Mg^{2}+	910	1800	760
Na+	1100	780	580
K+	680	660	110
Total	4990	6440	3050
Mineral anions			
SO_4^{2-}	990	2700	1010
NO_3^{-}	5	150	1
Cl^{-}	240	260	71
Total[a]	1235	3110	1082
Cations – mineral anions	3755	3330	1968
Organic anions[b]	2700–3200	1400–1700	1200–1400

[a]Excluding HCO_3^{-}.
[b]Estimated using the method of Oliver et al. (1983) for a pH of runoff varying between 5.0 (the lower value) and 6.0 (the higher value).

Mauricie. In general, there was a tendency for higher divalent cation, SO_4^{2-}, and NO_3^{-} export rates from burnt drainage areas and higher DOC export rates from harvested drainage areas. The Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, Cl^{-}, and TP export rates were positively related to the percentage of the drainage area that had been harvested. The K^{+}, Cl^{-}, TP, and TN export rates, when standardized by D_d, were similar in harvested and burnt drainage areas. Export rates were highest in the year following the disturbances but were still above rates in reference drainage areas 3 years later.

An increased export rate of DOC can be an important consequence of forest harvesting in Boreal Shield forests. Plamondon et al. (1982) observed a twofold increase in color (a surrogate to DOC in Shield runoff; Molot and Dillon 1997) following harvesting with a 10-m buffer strip in a Haute-Mauricie stream and a fourfold increase without a buffer strip. Nicolson (1975) also reported an increase in color and in DOC concentration in stream runoff from harvested Shield basins in northwestern Ontario. Increases in DOC or color exports following forest fires have not been reported. Unlike patterns in inorganic ion flux, DOC export rates were not related to the proportion of the drainage area harvested. However, DOC concentration in harvested lake basins was well predicted by simple empirical impact mod-

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Table 8. Element export (equiv. or mol·ha^{-1}·year^{-1}) in runoff from forested Precambrian Shield basins.

	Haute-Mauricie reference basins, Québec (mean and range)	ELA, Ontario	TLA, Ontario	Dorset, Ontario (mean and range)	Sogndal, Norway
Ca^{2}+	521 (353–823)	232	1188	—	161
Mg^{2}+	253 (175–389)	174	236	—	91
Na+	193 (126–270)	116	157	—	425
K+	37 (10–86)	20	46	—	35
SO_4^{2-}	339 (212–516)	76	767	—	209
NO_3^-	— (<5–8)	2.5	211	—	9
Cl^-	24 (17–70)	15	61	—	409
TP	4.3 (2.8–6.4)	1.3	—	2.6 (0.6–8.2)	—
TN	116 (40–174)	66	—	—	—
DOC	4800 (3130–6890)	2900	—	3900 (825–7600)	—
Reference[a]	1	2, 3	2	4	2

Note: The TLA and Dorset area receive moderate to elevated acid rain inputs. The Sogndal catchment is under maritime influence (i.e., elevated sea-salt inputs).

[a]1, this study; 2, Allan et al. (1993); 3, Bayley et al. (1992) (Rawson Lake northwest inflow); 4, Dillon and Molot (1997).

els taking into account the size of the drainage area and lake volume in addition to the percentage of the drainage area that had been disturbed (Carignan et al. 2000).

A combination of factors may be responsible for increased DOC export rates following forest harvesting in Haute-Mauricie. DOC production rates may increase in harvested areas because of increased organic matter decomposition rates in exposed forest floors and the input of fresh logging debris (Startsev et al. 1998). In addition, a higher water table generated by decreased evapotranspiration rates will favor increased DOC export because a larger proportion of runoff will bypass the DOC-sorbing mineral soil (Hinton et al. 1997). While increased water table height should also occur in burnt drainage areas, a large part of the forest floor can be lost by combustion during fires (MacLean et al. 1983). In addition, charcoal particles added to the forest floor following fires may sorb a portion of the DOC produced there (Wardle et al. 1998). The topographical properties of drainage areas should exert some control over DOC losses following harvesting through their influence on seasonal waterlogging (D'Arcy and Carignan 1997). In other words, some drainage areas may be more susceptible than others to increased DOC export rates following harvesting. We hypothesize that increases in DOC export rates will be greatest in drainage areas where seasonal waterlogging is important and when harvested areas intersect the zone of seasonal saturation.

Contrasts in nutrient export mechanisms between harvested and burnt basins

The patterns in N, P, and S flux between harvested and burnt drainage areas may be more complex than our measurements suggest because these elements can be exported in both organic and inorganic forms. For example, assuming a DOC:DON ratio of ~55 in Shield stream water (Allan et al. 1993), DON exports represented ~82% of cumulative TN exports for harvested drainage areas, ~46% for burnt drainage areas, and ~73% for reference drainage areas. Thus, while cumulative TN exports were similar between burnt and harvested drainage areas, N was exported mostly in organic forms following harvesting and in both mineral and organic forms following fires. The increased export of DOC from harvested basins indicates that the export of DON, S, and P probably increased as well.

Different mechanisms were responsible for the transport of base cations from the forest to the lakes in harvested and burnt basins. The magnitude of cation export from drainage areas is controlled by the availability of mobile anions (Reuss and Johnson 1986). In reference drainage areas, dissociated organic acids (i.e., a component of DOC) and SO_4^{2-} were the two important anions in runoff (Table 7). In contrast, SO_4^{2-} was the dominant anion in runoff from burnt drainage areas and dissociated organic acids the main anions in runoff from harvested drainage areas. Even when their export increased, Cl^- and NO_3^- were only a small component of the anion flux. Thus, although base cation export increased in both harvested and burnt drainage areas, the mechanisms involved were different. Increased base cation export was caused by increased leaching of inorganic anions in burnt basins and increased leaching of organic anions in harvested basins.

Element export from reference drainage areas

Element export rates estimated from Haute-Mauricie reference drainage areas fall within the range found in other small Precambrian Shield basins (Table 8). In general, the pattern in the export of major cations and anions from Haute-Mauricie drainage areas is intermediate between patterns found at the Experimental Lakes Area (ELA) and the Turkey Lakes Area (TLA), both in Ontario. The ELA is located in a relatively pristine area of the Precambrian Shield, while the TLA receives important S inputs of anthropogenic origin. At the three sites, Ca^{2+} and Mg^{2+} are the main cations in runoff. However, the amount of Ca^{2+} exported is variable between sites and appears to be related to SO_4^{2-} export. The Ca^{2+} and SO_4^{2-} exports are lowest at the ELA, intermediate in Haute-Mauricie, and highest at the TLA. A gradient in SO_4^{2-} deposition also occurs within the Haute-Mauricie region, and SO_4^{2-} export rates in reference basins were positively related to wet SO_4^{2-} deposition rates (export (equivalents per hectare per year) = –65 + 1.5 × wet deposition (equivalents per hectare per year); $P = 0.02$, $r^2 = 0.34$). Most reference Haute-Mauricie drainage areas exported

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Table 9. Nutrient losses ($kg \cdot ha^{-1}$) following forest fires or harvesting in Boreal Shield forests.

	Fire		Harvesting		
	Volatilization[a]	Runoff[c]	*Picea mariana*[d]	*Betula papyrifera*[d]	Runoff[c]
Ca	72	32	130–190	93–210	14
Mg	20	13	6–15	14–31	1.8
K	19	22	24–57	37–91	22
N	445	5.0	28–110	84–160	5.0
P	<40[b]	0.4	34–47	4–14	0.3

[a]Estimated from soil pits (forest floor and 0–20 cm mineral soil) in areas burnt during the 1995 Belleplage fire relative to nearby reference areas in 1996 (Brais et al. 2000). Volatilization losses were approximated as the difference in nutrient mass between soil pits from burnt and reference areas minus the average nutrient export in runoff from burnt areas in 1996 (this study). The Belleplage fire occurred within the study area.

[b]From MacLean et al. (1983).

[c]Difference in cumulative exports between disturbed (as D_d) and reference drainage areas from 1996 to 1998 in this study.

[d]Bole (lower boundary) and bole plus branches (upper boundary) biomass at the time of harvest for pure stands in Québec (D. Paré, unpublished data from several sources).

more SO_4^{2-} than was supplied by wet deposition, suggesting an important dry deposition component or desorption of past S inputs (Houle and Carignan 1995). Patterns in cation and anion flux are markedly different between Haute-Mauricie and the Sogndal catchments in Norway, which are under a maritime influence. Overall, the patterns in element flux in reference Haute-Mauricie drainage areas are consistent with a continental Precambrian Shield setting subjected to past or present anthropogenic S inputs.

Significance of nutrient export in runoff to forest and lake nutrient budgets

The cumulative loss of nutrients in runoff for the 3 years following the disturbances was compared with losses through volatilization during fires and through biomass removal during harvesting (Table 9). The losses in runoff used here are minimum estimates because elevated exports will likely occur for several more years. Potassium was the element with the highest loss in runoff relative to volatilization or biomass removal (19% to 54% of total losses). Calcium and Mg losses in runoff were of intermediate importance, representing 5–39% of total losses. Losses of N and P in runoff were small relative to losses through volatilization or biomass removal (1–15% of total losses). Similar patterns in base cation exports were observed following forest fires (Bayley and Schindler 1991) and harvesting (Nicolson et al. 1982) at the ELA. Overall, losses through runoff following disturbances were more important for base cations than for N and P in Haute-Mauricie forests. Even though the processes of nutrient removal are different between forest harvesting and fire, with the exception of whole-tree harvesting (i.e., bole and branches), cumulative losses of base cations are relatively similar between these two disturbances. Whole-tree harvesting nearly doubled the losses of Ca and Mg in Haute-Mauricie forests.

While the increase in N and P export rates in runoff following harvesting or fires appeared to be a negligible loss of nutrient for the forest, they represented a significant input to lakes. Relative to the loading rates predicted from the D of reference drainage areas, the load of TN and TP increased by 33 and 64%, respectively, in lakes in burnt basins and by 41 and 58%, respectively, in lakes in harvested basins (S. Lamontagne, unpublished data). The P load is a strong determinant of total primary production in Shield lakes, while the N:P ratio can influence the composition of algal populations (Schindler 1977). Pelagic and especially benthic algal biomass was higher in burnt and harvested lake basins relative to reference lake basins (Planas et al. 2000). Zooplankton biomass was higher in burnt lake basins in the second year following the disturbance, while calanoid copepod biomass was lower in harvested lake basins in the first year (Patoine et al. 2000). Thus, the inferred increases in element export rates in disturbed basins were also accompanied by changes at higher trophic levels.

Clearcuts over large areas are often justified on the grounds that natural disturbance, such as forest fires, also removes trees over large surfaces. However, for the export of elements from forests to lakes, forest harvesting and forest fires are not similar disturbances in Haute-Mauricie. An important difference between these disturbances is the potential for an increased DOC export following harvesting but not following fires. DOC is one of the key variables in the ecology of Boreal Shield lakes (Schindler et al. 1992, 1997). DOC participates in the transport (Bayley et al. 1992; Allan et al. 1993) and cycling of nutrients in Shield lakes (Schindler et al. 1992). DOC from terrestrial sources is colored and is a strong determinant of the optical properties of Shield waters (Fee et al. 1996). In small Shield lakes (<500 ha), DOC is the primary determinant of thermocline depth (Fee et al. 1996). In this study, light extinction coefficients were higher in harvested lake basins due to higher epilimnetic concentrations of colored DOC (Carignan et al. 2000). Increased DOC export following harvesting could affect the transport and cycling of some contaminants, such as methyl mercury (Garcia and Carignan 1999).

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Mercury concentrations in northern pike (*Esox lucius*) from boreal lakes with logged, burned, or undisturbed catchments

Edenise Garcia and Richard Carignan

Abstract: We measured total Hg and stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) in northern pike (*Esox lucius*) from 19 Boreal Shield lakes with undisturbed, logged, or burned watersheds. Average Hg level in standard 560-mm northern pike, on a dry weight basis, was significantly higher in logged lakes (3.4 $\mu g \cdot g^{-1}$) than in reference lakes (1.9 $\mu g \cdot g^{-1}$). Average Hg concentrations in burned lakes (3.0 $\mu g \cdot g^{-1}$) did not differ significantly from those in logged and references lakes. Concentrations of Hg normalized to trophic position determined from isotopic composition yielded similar results. Mercury levels were above the WHO safe consumption limit in all logged lakes. Mercury in northern pike was correlated with methyl mercury in zooplankton (+), total N (+), pH (–), alkalinity (–), sulfate (+), dissolved organic C loading (+), and light attenuation in lake water (+). Stepwise multiple regressions explained 79% of the variability in Hg in fish and included methyl mercury in zooplankton, pH, and sulfate as independent variables. Explained variability increased to 92% when a second-order lake with an exceptionally large drainage area was excluded. Our results suggest that extensive logging activities may disrupt the natural cycling of Hg in watersheds and increase Hg levels in the aquatic biota.

Résumé : Nous avons mesuré le Hg total et les isotopes stables ($\delta^{13}C$ et $\delta^{15}N$) chez le grand brochet (*Esox lucius*) de 19 lacs de la forêt boréale dont le bassin versant avait été coupé, brûlé ou n'avait pas subi de perturbation. Les niveaux moyens en Hg chez le grand brochet de 560 mm de longueur étaient significativement plus élevés dans les lacs coupés (3,4 $\mu g \cdot g$ poids sec^{-1}) par rapport aux lacs de référence (1,9 $\mu g \cdot g$ poids sec^{-1}). La concentration moyenne en Hg chez le grand brochet des lacs brûlés (3,0 $\mu g \cdot g$ poids sec^{-1}) ne différait pas significativement de celle des lacs coupés ou de référence. Des résultats semblables ont été obtenus à partir des concentrations en Hg normalisées pour la position trophique, déterminée à partir des isotopes stables. Les niveaux de Hg dépassaient la limite récommendée par l'OMS pour la consommation humaine dans tous les lacs coupés. Le Hg chez le grand brochet était corrélé avec le méthyl mercure chez le zooplancton (+), le N total (+), le pH (–), l'alcalinité (–), le sulfate(+), les apports en C organique dissous (+) et la pénétration de lumière dans l'eau (+). Un modèle de régression multiple incluant le méthyl mercure chez le zooplancton, le pH et le sulfate comme des variables indépendantes a expliqué 79% de la variation de la concentration en Hg chez le grand brochet. Le modèle résultant de l'exclusion d'un lac de second ordre ayant une aire de drainage exceptionnellement grande a expliqué 92% de la variabilité du Hg chez le grand brochet. Nos résultats suggèrent que la coupe forestière extensive peut perturber le cycle naturel du Hg des bassins versants et augmenter l'accumulation de ce métal dans la biote aquatique.

Introduction

Several environmental and biological factors can affect the accumulation of Hg in fish, including lake productivity (Hill et al. 1996), pH, alkalinity, sulfate and Ca concentrations (Hudson et al. 1994), trophic position (Cabana et al. 1994), and age and growth (MacCrimmon et al. 1983). Humic matter, in particular, has been inferred as an important vector of Hg from topsoils to lakes and streams (Kalbitz and Wennrich 1998; Kolka et al. 1999), and this may explain observed relationships between water color or dissolved organic C (DOC) and Hg concentration in aquatic biota. Forest removal by fire or clear-cutting affects runoff and DOC loading to lakes (Hobbie and Likens 1973; Lamontagne et al. 2000). Such disturbances may therefore also influence the loading of organic matter bound Hg to lakes.

In a previous study of 38 remote Boreal Shield lakes, we observed that methyl mercury (MeHg) levels were significantly higher in zooplankton in lakes with partially clearcut watersheds than in lakes with burned or undisturbed watersheds (Garcia and Carignan 1999). MeHg in zooplankton was correlated most strongly with DOC concentration. In the present study, we report total Hg concentrations in northern pike (*Esox lucius*), a top predatory fish, which was found in 20 of the 38 lakes.

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Materials and methods

Study site

The study was conducted in 20 lakes on the Canadian Shield,

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near Gouin Reservoir (central Quebec, 48°50′N, 75°00′W), at the transition between the boreal mixed and coniferous forests (see detailed description and map in Carignan et al. 2000). Wetlands, which are important sources of DOC, represent less than 6% of the drainage area (average = 1.8%) of the study lakes. All lakes but one (FP15) are headwater lakes. The 20 lakes include nine reference lakes (N43, N55, N56, N59, N63, N88, N89, N107, and N122), four logged lakes (C2, C9, C24, and C40), and seven burned lakes (FP2, FP15, FP24, FP30, FP32, FBP9, and FBP10). Catchment areas of reference lakes had remained undisturbed for at least 40 years. Logging and fires occurred in 1995. The logged lakes had between 11 and 72% (average = 43%) of their catchment area clearcut. Harvesting continued after 1995 in the watershed of Lake C2, increasing the cleared fraction from 31 to 72% of the watershed. Logged area to lake area ratios varied from 0.4 to 6.1 (average = 3.2). Fires affected more than 90% of the catchment area of six lakes and 50.1% of the catchment of one lake.

Water chemistry and morphometric data

The lakes were sampled during the summers of 1996, 1997, and 1998. Duplicate integrated samples were taken from the euphotic zone and were analysed using standard methods (Carignan et al. 2000). Measured properties included light attenuation, Secchi depth, DOC, dissolved oxygen, pH, alkalinity, total P and N, sulfate, Ca, and chlorophyll *a*. DOC loading to the lakes (moles C per square metre per year) was estimated for the 3 years following disturbances (Lamontagne et al. 2000).

Morphometric variables were determined from topographic maps (1:20 000) and from aerial photographs (1:15 000). Variables included drainage area, lake area, lake volume, maximum depth, the extent of perturbation by logging or fire and the percentage of wetlands in the catchment.

Sample collection

Fish were collected during the summer of 1996 or 1997. Seven lakes were resampled during the summer of 1998 (C2, C9, FP24, FBP10, N55, N63, and N107). Between six and 23 specimens were collected in each lake, for a total 312 northern pike. Total length, weight, and sex were recorded for all fish.

Benthic organisms for stable isotope analysis were sampled during the summer of 1999 in the littoral zone (<2 m deep) of each lake using hand-held dip nets. Invertebrates were sorted, identified to the level of suborder or family, counted, and kept frozen until freeze-dried. Only nonpredatory organisms (primary consumers) were considered. The organisms were divided into four taxonomic groups: Amphipoda, Trichoptera, Ephemeroptera, and Chironomidae.

Zooplankton data for the same lakes were taken from Garcia and Carignan (1999). MeHg concentrations in zooplankton are averages for samples collected in June, July, and September of 1996.

Mercury analysis

A boneless, skinless fillet of dorsal muscle tissue was removed from each fish, frozen, and freeze-dried. Subsamples (0.1 g) of fish tissue were analysed using the hot acid extraction method of Hendzel and Jamieson (1976). Mercury analysis was performed by cold-vapor atomic absorption spectrophotometry. Twenty samples analysed in duplicate had an average coefficient of variation of 4%. Certified reference material (DORM-2, National Research Council of Canada) was run every 25 samples, and recoveries averaged 4.72 ± 0.21 mg·kg^{-1} (N = 12), which corresponds to 105 ± 4.6% of the certified value (4.47 ± 0.32 mg·kg^{-1}). Concentrations are reported as micrograms per gram of dry weight. A conversion factor of 0.2 was used to express concentrations on a wet weight basis.

Isotopic analysis and determination of northern pike trophic position

In order to correct for the among-lake variability in Hg concentrations due to food chain length, Hg levels were normalized as a function of trophic position (Λ), as defined using stable C and N isotope ratios (Vander Zanden and Rasmussen 1999).

Stable C and N analyses were performed on 255 samples of 0.7 mg of dried fish muscle and zoobenthos subsamples. The analyses were conducted using a continuous-flow Isoprime isotope ratio mass spectrometer coupled with an elementary analyser (NC 1500) at the GEOTOP Laboratory (Université du Québec à Montréal). Stable isotope values are expressed in δ notation as parts per thousand deviation from a standard reference:

$$\delta^{13}C \text{ or } \delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Standard references were Pee Dee Belemnite limestone for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$. We assumed that $\delta^{15}N$ increases on average 3.4‰ per trophic level (Cabana and Rasmussen 1994). Variations in baseline $\delta^{15}N$ values from lake to lake were corrected for using the method proposed by Vander Zanden and Rasmussen (1999). This method takes into account the $\delta^{15}N$ and $\delta^{13}C$ relationship found in primary consumers (pcons):

$$(1) \qquad \delta^{15}N_{pcons} = \frac{6.34}{1 + e^{9.67 + (0.356\delta^{13}C_{pcons})}}$$

For each primary consumer, the residual from eq. 1 (U_{res}) is calculated by subtracting the value given by the equation from the measured $\delta^{15}N$. For each lake, an average residual ($\overline{U}_{res}$) of all primary consumers is then calculated. Next, the measured $\delta^{13}C$ of each fish from a given lake is entered into eq. 1 and a $\delta^{15}N$ is estimated. The $\overline{U}_{res}$ for that lake is then added to the estimated $\delta^{15}N$. The value thus obtained is the lake-corrected baseline $\delta^{15}N$ ($\delta^{15}N_{corrected}$), which is specific for each individual fish. Finally, the trophic position of the fish is given by the equation

$$(2) \qquad \Lambda_{pike} = \left[\frac{(\delta^{15}N_{pike} - \delta^{15}N_{corrected})}{3.4}\right] + 2$$

where Λ_{pike} is the trophic position and $\delta^{15}N_{pike}$ is the $\delta^{15}N$ measured for each fish. The constant 3.4 is the $\delta^{15}N$ increment per unit of trophic level, and the constant 2 corresponds to the trophic level of primary consumers.

Data analysis

We compared Hg concentrations in northern pike from the three groups of lakes using two different approaches. First, we regressed Hg concentrations in northern pike against fish total length (average R^2 = 0.85) for each lake. In all but one lake (N59), where no significant relationship was observed, these regression equations were used to estimate Hg levels for a standard length of 560 mm. This value represented the mean total length for all fish and corresponded to a northern pike weighing 1.08 kg. Reference Lake N59 was excluded from the analyses because no significant relationship was found between Hg concentration and fish length. Lake N59 had the smallest sample size (N = 6) and the largest mean fish total length (600 mm).

Second, we regressed trophic position against fish total length and determined trophic position for a standard 560-mm fish in each lake. Mercury concentrations in standard 560-mm northern pike were normalized as a function of trophic position by dividing estimated Hg concentrations by the estimated trophic position of standard 560-mm fish.

Differences among treatments were tested using a nonparametric Kruskal–Wallis test. Pearson correlation coefficients were calcu-

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Table 1. Mercury concentrations in 560-mm northern pike (Hg), northern pike trophic position (Λ), and Hg levels normalized to trophic position (Hg/Λ) in all study lakes (N = 19).

Lake	Treatment	Hg (μg·g dry weight^{-1})	Λ	Hg/Λ (μg·g dry weight^{-1}·Λ^{-1})
C2	Logging	3.4	4.42	0.77
C9	Logging	2.7	4.22	0.64
C24	Logging	4.2	4.29	0.98
C40	Logging	3.0	4.41	0.68
FP2	Fire	6.4	4.24	1.51
FP15	Fire	1.8	3.00	0.60
FP24	Fire	2.6	4.56	0.57
FP30	Fire	4.4	3.58	1.23
FP32	Fire	2.0	3.77	0.53
FBP9	Fire	1.3	3.71	0.35
FBP10	Fire	2.2	3.73	0.59
N43	Reference	2.5	4.31	0.58
N55	Reference	1.5	4.29	0.35
N56	Reference	2.4	4.14	0.58
N63	Reference	2.2	3.73	0.59
N88	Reference	1.8	3.33	0.54
N89	Reference	0.9	4.09	0.22
N107	Reference	2.2	3.86	0.57
N122	Reference	1.5	4.29	0.35

lated between Hg in northern pike and morphometric, chemical, and biological variables. Stepwise multiple linear regression was used to define empirical relationships between Hg in fish and environmental and biological variables. For the lakes sampled twice, only the data obtained during the first sampling year were included in these analyses. When necessary, data were log transformed to achieve normality and homoscedasticity.

Results

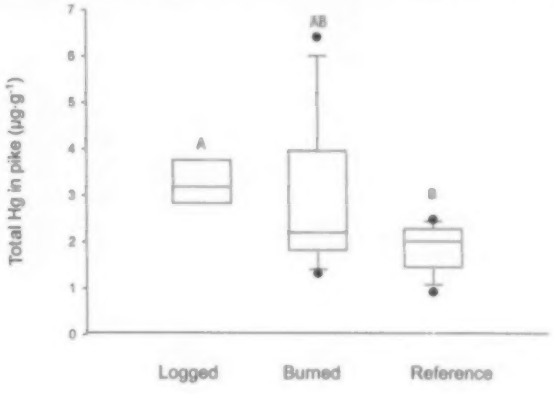
Mercury in northern pike

On a dry weight basis, Hg concentrations in 560-mm northern pike ranged from 0.9 to 6.4 μg·g^{-1} (Table 1). The three treatments showed significantly different levels of Hg in northern pike (p = 0.047). In logged lakes, Hg concentrations averaged 3.4 μg·g^{-1} and were significantly higher than in reference lakes (mean concentration of 1.9 μg·g^{-1}) (Fig. 1). The average Hg concentration in northern pike from burned lakes (3.0 μg·g^{-1}) was intermediate between the levels observed in logged and in reference lakes, but differences were not significant. Note, however, that the highest Hg concentration was found in a lake with a partially (50.1%) burned watershed. When this lake is removed from the analysis, the mean Hg levels in burned lakes decrease to 2.4 μg·g^{-1}.

The $\delta^{13}C$ and the $\delta^{15}N$ of benthic invertebrates were highly variable, ranging from –32.9 to –24‰ and from –2.4 to + 4.4‰, respectively. The variation in $\delta^{15}N$ is equivalent to two trophic levels. The $\delta^{13}C$ and the $\delta^{15}N$ of northern pike ranged from –30.7 to –25.8‰ and from +7.1 to +10.7‰, respectively.

The trophic position of 560-mm northern pike, adjusted for variations in baseline $\delta^{15}N$–$\delta^{13}C$ between lakes, ranged from 3.0 to 4.6 (Table 1) and tended to be higher in logged lakes, but differences among treatments were not significant.

Fig. 1. Box plots showing median values and 10th, 25th, 75th, and 90th percentiles of Hg in 560-mm northern pike, expressed on a dry weight basis, from logged (N = 4), burned (N = 7), and reference lakes (N = 8). Letters on top of the boxes indicate between-treatment differences: boxes with different letters are significantly different (Wilcoxon–Mann–Whitney test, $p < 0.01$).



Mercury concentrations normalized to trophic position in northern pike from reference, logged, and burned lakes were again significantly different, but this time at a p level of 0.025. These results indicate that among-group variations in trophic position were not responsible for the observed differences in Hg concentrations in northern pike.

Relationships between Hg concentrations in northern pike and environmental variables

Significant differences were observed between the three groups of lakes for several morphometric, water quality, and biological variables (Table 2). Lakes with burned watershed showed significantly higher levels of chlorophyll *a*, TP, TN, and sulfate compared with logged and reference lakes. Lake water pH in the study lakes was circumneutral and was slightly lower, although not significantly ($p > 0.05$), in logged lakes relative to burned and reference lakes. The drainage areas of logged lakes exported more DOC compared with burned and undisturbed lakes, and DOC concentrations were the highest in logged lakes. Watershed properties of the three groups of lakes only differed with respect to the mean drainage area due to the inclusion in the burned group of one lake (FP15) that has a larger headwater lake in its watershed and has an exceptionally large drainage area.

Significant correlations were found between Hg concentrations in 560-mm northern pike and some environmental and biological characteristics of the study lakes (Table 3). Mercury in northern pike showed the strongest relationship with MeHg in zooplankton (Fig. 2). Other variables also significantly correlated with Hg were pH (–), alkalinity (–), sulfate (+), TN (+), and light attenuation (+), which was itself highly correlated with DOC loading (r = 0.92, $p < 0.0001$). The relationships between Hg in northern pike and three intercorrelated variables, DOC loading from the drainage area, DOC in lake water, and drainage ratio, only became significant (r = 0.61, 0.50, and 0.48, respectively, $p < 0.05$)

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Table 2. Physical, chemical, and morphometric characteristics of the study lakes and their catchments.

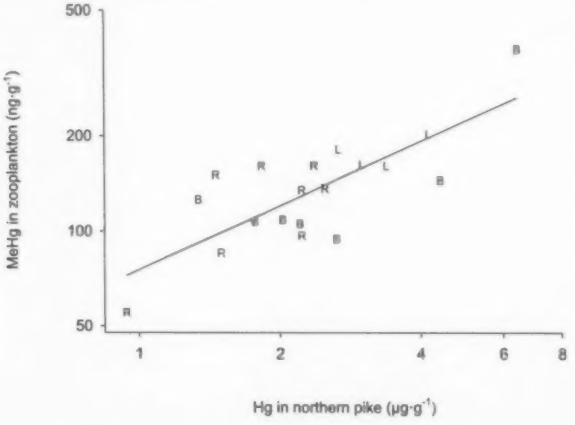
	Reference (N = 8)				Burned (N = 7)				Logged (N = 4)			
	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
Lake area (km^2)	0.4	0.2	0.2	0.7	0.4	0.1	0.2	0.6	0.4	0.2	0.2	0.7
Drainage area (km^2)	2.4	1.3	0.9	4.5	5.2	6.6	0.6	19.7	3.1	2.0	1.0	5.9
Maximum depth (m)	11.9	4.9	7.0	23.0	14.1	3.2	10.0	20.0	18.2	8.5	12.0	30.0
Lake volume (km^3)	1.9	1.3	0.6	4.0	1.9	1.0	0.7	3.5	1.9	1.4	0.6	3.8
% of drainage area as wetlands	2.4	2.6	0	6.0	1.1	1.3	0	3.6	1.8	1.2	0	3.0
Disturbed area to lake area	0	0	0	0	11.7	9.2	3.3	40.4	4.0	3.4	0.4	6.1
pH	6.6	0.3	6.3	7.0	6.5	0.4	5.7	7.2	6.1	0.3	5.9	6.6
Alkalinity ($\mu equiv.\cdot L^{-1}$)	70.7	29.5	32.0	110.0	66.4	41.3	17.2	146.1	34.7	15.6	15.3	47.6
DOC loading to lakes (mol C·m $lake^{-2}\cdot year^{-1}$)	3.4	2.5	1.4	9.3	6.9	6.4	1.6	20.3	7.0	5.6	1.4	9.3
DOC ($mg\cdot L^{-1}$)	5.7	1.6	3.6	9.2	6.2	1.6	4.0	8.0	7.4	3.1	4.2	11.1
Light attenuation coefficient (m^{-1})	1.0	0.3	0.7	1.7	1.1	0.4	0.6	1.8	1.5	0.7	1.0	2.5
Secchi depth (m)	3.6	0.8	2.2	5.0	3.1	1.4	2.1	5.6	2.9	1.2	1.6	4.2
Chlorophyll *a* ($\mu g\cdot L^{-1}$)	1.9	0.4	1.1	2.3	3.2	1.1	1.6	4.7	2.0	0.6	1.3	2.7
TP ($\mu g\cdot L^{-1}$)	6.6	1.7	4.7	9.5	11.7	2.6	8.4	15.3	9.1	2.3	6.9	12.4
TN ($\mu g\cdot L^{-1}$)	223.8	43.6	149.5	294.0	311.1	83.0	217.0	440.0	237.3	58.8	160.0	303.0
Ca^{2+} ($mg\cdot L^{-1}$)	1.8	0.5	1.2	2.5	2.1	0.5	1.4	2.7	1.6	0.3	1.2	2.0
SO_4-S ($mg\cdot L^{-1}$)	0.8	0.2	0.6	1.0	1.5	0.3	1.1	2.1	0.9	0.1	0.8	1.0
MeHg in zooplankton ($ng\cdot g$ dry $weight^{-1}$)	122.3	38.9	55.1	160.6	151.8	100.5	94.2	376.7	176.8	19.8	160.5	203.0

Table 3. Pearson correlation coefficients observed between log Hg concentrations in 560-mm northern pike and environmental and biological characteristics of the study lakes and watersheds (N = 19).

	r	p
Lake area	–0.38	0.109
log drainage area	–0.11	0.639
log drainage area/lake area*	0.48	0.048
Alkalinity	–0.57	0.011
pH	–0.66	0.002
log DOC loading*	0.61	0.009
log DOC*	0.50	0.034
log light attenuation coefficient*	0.52	0.021
Chlorophyll *a*	0.03	0.904
TP	0.33	0.173
TN	0.51	0.026
Ca^{2+}	–0.28	0.244
SO_4^{2-}	0.49	0.038
log MeHg in zooplankton	0.77	0.000

*Excluding Lake FP15.

Fig. 2. Relationship between Hg concentrations in 560-mm northern pike and MeHg concentrations in zooplankton, expressed on a dry weight basis (r = 0.79, p = 0.0000, N = 19 lakes). L, logged lakes (N = 4); B, burned lakes (N = 7); R, reference lakes (N = 8).



following the exclusion of second-order Lake FP15 from the regressions.

Stepwise multiple regressions including all lakes showed that MeHg in zooplankton, sulfate, and pH explained 79% of the variance in Hg concentrations in northern pike (Table 4, eq. T1). MeHg in zooplankton alone explained 61% of the variation. When Lake FP15 was removed from the set of lakes, pH and sulfate remained in the model, and DOC export rate replaced MeHg in zooplankton. This alternative regression model (Table 4, eq. T2) was highly significant, and its R^2 increased to 0.92. Lake pH explained a larger amount of the variation in Hg than sulfate and DOC in this regression. DOC loading and MeHg in zooplankton were correlated and mutually exclusive as independent variables in our regression models.

Temporal trends of Hg in northern pike

In lakes sampled twice, Hg concentrations varied between the first and the second sampling year, but differences were not significant (paired t test, $p > 0.05$). In one of the two

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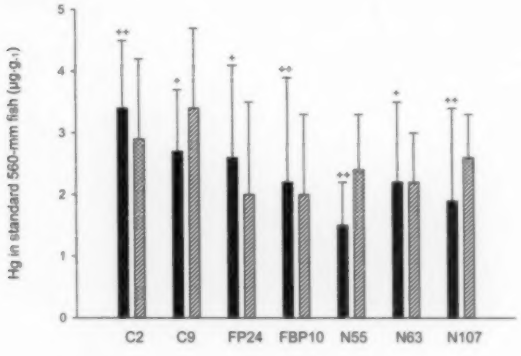
Table 4. Multiple regression models for Hg concentrations in northern pike (μg·g dry weight^{-1}).

(T1) log Hg = –0.23±1.70 + 0.58±0.16 log MeHgzoop** + 0.43±0.12(SO_4^{2-})** – 0.34±0.17(pH)*
$R^2_{adjusted}$ = 0.79, SE_{est} = 0.14, p = 0.0000, N = 19 lakes
(T2) log Hg = 1.44±0.89 – 0.62±0.09(pH)*** + 0.56±0.08(SO_4^{2-})*** + 0.27±0.05 log DOC loading***
$R^2_{adjusted}$ = 0.92, SE_{est} = 0.13, p = 0.0000, N = 18 lakes

Fig. 3. Temporal trends in levels of Hg in 560-mm northern pike, expressed on a dry weight basis, from two logged (C2 and C9), two burned (FP24 and FBP 10), and three reference lakes (N55, N63, and N107) sampled twice: in 1996 (solid bars, +) or in 1997 (solid bars, ++) and in 1998 (hatched bars). Lines above the bars represent the standard error of estimated Hg for 560-mm northern pike.



logged lakes resampled in 1998 (C9), the estimated Hg concentration in standard 560-mm fish increased by about 28%, whereas it remained the same in the other lake (C2) (Fig. 3). In burned lakes, an average decrease of 18% was observed. In two reference lakes (N63 and N107), Hg concentrations in northern pike showed little variation from one year to another. In a third reference lake (N55), Hg concentrations were higher in 1998 than in 1997.

Discussion

Mercury concentrations in 560-mm northern pike from our lakes, on a wet weight basis, were comparable with those observed by Håkanson et al. (1988) in 1-kg pike from 1456 Swedish lakes and by Bodaly et al. (1993) in 600-mm pike from six Canadian Shield lakes. They were lower, however, than concentrations reported by Parks et al. (1994) for 550-mm pike from 42 pristine lakes in northern Minnesota, U.S.A. In all logged lakes, Hg concentrations in 560-mm northern pike were higher than the advisory limit for human consumption of 0.5 μg·g wet weight^{-1} of the World Health Organization. This limit was exceeded in three burned lakes and in only one reference lake.

As previously observed for MeHg in zooplankton collected in the same lakes (Garcia and Carignan 1999), Hg in northern pike was highest in fish from logged lakes. As indicated by the regression models, Hg in northern pike increased with increasing DOC loading and with concentrations of sulfate in lake water and declined with increasing lake water pH. These three factors are related either to Hg transfer to lakes or to microbial methylation rates. The variables selected in our regression models are in accordance with the Hg cycling model of Hudson et al. (1994), where DOC, pH, and sulfate in conjunction with Ca are the limnological characteristics that most directly affect Hg levels in fish.

Lake water pH was the most important predictor of Hg concentrations in northern pike. The average pH of logged lakes (6.1) was slightly lower than that of burned (6.5) and reference lakes (6.6). This difference in pH may partially explain differences in Hg among treatments. In reference lakes, Hg concentrations showed a negative (r = –0.69) and nearly significant (p = 0.058) correlation with pH. The slope of this relationship (–1.4 ± 0.6) indicates that a variation of 0.5 pH unit, as that observed between logged and reference lakes, may be responsible for a variation of around 0.7 ± 0.3 μg·g^{-1} in Hg concentration. This pH effect is commonly observed (Jensen 1988; Ponce and Bloom 1991) and may be due to several mechanisms. At low pH, the exchange of H^+ with humic acid bound Hg^{2+} may increase the availability of Hg^{2+} and increase its methylation rate (Xun et al. 1987). High pH, on the contrary, enhances the reduction of Hg^{2+} to the volatile Hg^0 (Hudson et al. 1994). Variations in pH may also interfere with uptake of both organic and inorganic Hg by aquatic organisms (Rodgers and Beamish 1983).

High Hg concentrations in fish from logged lakes may be partly attributed to variations in Hg inputs associated with the loading of terrestrial DOC. In these lakes, one of the most noticeable effects of logging was a pronounced increase in the DOC export from the drainage area. The role of the organic matter in the mobilization and translocation of heavy metals, including Hg, from watersheds to aquatic ecosystems is well known (Meili 1991; Kalbitz and Wennrich 1998). The effects of organic matter on lake Hg and MeHg levels are complex, however. Some studies have shown that DOC increases Hg bioavailability in lakes by stimulating microbial methylation rates (McMurtry et al. 1989) and by retaining Hg in the water column. Hecky et al. (1991) observed that the addition of terrestrial debris, including spruce boughs and boreal forest floor materials, to mesocosms increased Hg concentrations in fish. Input of DOC may also decrease the rates of photodegradation of MeHg in lakes (Sellers et al. 1996). These studies support the positive relationship between Hg concentrations in fish and DOC observed in our lakes. In contrast, Grieb et al. (1990) observed a negative relationship between DOC or water color and Hg in fish, especially in clear-water lakes. This phenomenon was attributed to the complexation of Hg species with sulfhydryl groups on organic molecules, which decreases the availability of Hg to the aquatic biota (Grieb et al. 1990) and inhibits methylation (Miskimmin at al. 1992).

The positive correlation between Hg levels in northern pike and sulfate concentrations may be related to the acidity of the lakes or to the methylation activity of sulfate-reducing bacteria (Gilmour and Henry 1991; Hudson et al. 1994). Sulfate concentrations were nearly identical in reference and

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logged lakes, however, and cannot explain the higher Hg concentrations measured in fish captured in logged lakes.

The highest Hg level was observed in a partially burned lake (FP2). Canavan (1998) observed five- and 20-fold increases in Hg and MeHg concentrations, respectively, in the sediment of a reservoir following a partial burn of its watershed. These higher concentrations were attributed to an increase in the loading of allochthonous organic matter as well as to increased Hg methylation. Lake FP2 also had a high DOC load (6.3 mol $C \cdot m^{-2} \cdot year^{-1}$) compared with the average value found for the other burned lakes (4.3 mol $C \cdot m^{-2} \cdot year^{-1}$, excluding Lake FP15). Note, however, that Lake FP2 also had the lowest pH.

Because MeHg can be biomagnified through the food web, trophic position is an important factor explaining among-lake differences in Hg concentrations in a given species (Cabana and Rasmussen 1994). In our lakes, however, variations in northern pike trophic position were relatively small and did not significantly influence the observed differences among logged, burned, and reference lakes. Nonetheless, the normalization of Hg concentrations as a function of trophic position did increase the level of significance of statistical tests used in the among-treatment comparisons. This normalization provides an alternative to conventional methods for comparisons of Hg concentrations in different fish species.

Differences between logged and reference lakes were noticed as early as 1 and 2 years after harvesting. This result suggests that fish may respond rapidly to environmental alterations of the Hg cycle, as reported by Hecky et al. (1991), who observed a 10-fold increase in Hg levels in yellow perch (*Perca flavescens*) 2 months after the addition of terrestrial organic materials to mesocosms. No clear trend was observed in Hg levels in 560-mm northern pike from the lakes sampled twice due to the small number of revisited lakes.

Our results suggest that extensive logging activities may increase Hg levels in northern pike. Increased DOC loads to impacted lakes may disrupt the natural cycling of Hg in watersheds and cause its accumulation in the aquatic biota. Partial loss of forest cover through fires may also cause elevated Hg levels in the biota. If confirmed by further studies, these effects should be taken into consideration in future forest harvesting practices.

Acknowledgments

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Pelagic and benthic algal responses in eastern Canadian Boreal Shield lakes following harvesting and wildfires

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Abstract: Pelagic and benthic algal biomass and pelagic algal community structure were measured in Boreal Shield lakes impacted by forest harvesting and wildfires (Haute-Mauricie, Québec). Sixteen reference lakes in which the watershed has been unperturbed for at least 40 years, seven harvested lake watersheds (logged in 1995), and nine lake watersheds burnt in 1995 were sampled for 3 years following harvesting or wildfires. From 1996 to 1998, repeated-measures ANOVA showed significant effects between treatment and sampling years for pelagic chlorophyll *a* (Chl *a*) and biomass, but for 1997–1998 benthic Chl *a*, repeated-measures ANOVA showed only significant treatment effects. Chl *a* concentrations increased 1.4- to 3-fold in perturbed lakes as compared with reference lakes. Areal pelagic Chl *a* (milligrams per square metre) was lower than estimated littoral Chl *a* in perturbed lakes. The pelagic algal community was dominated by mixotrophic nanoflagellates in reference lakes. Watershed perturbation induced differential changes in pelagic algal communities: mixotrophic nanoflagellates increased in harvested lakes and photoautotrophic diatoms in burnt lakes. Considering only perturbed lakes, algal biomass was proportional to the fraction of the catchment area perturbed divided by the surface area of lakes in the catchment.

Résumé : La biomasse des algues pélagiques et benthiques ainsi que la structure de la communauté pélagique ont été mesurées dans 32 lacs de la forêt boréale (Haute-Mauricie, Québec) : seize lacs de référence non perturbés depuis au moins 40 ans, sept lacs ont été perturbés par des coupes forestières (1995) et neuf lacs dont les bassins versants ont subi des feux de forêt (1995). Pour la chlorophylle *a* (Chl *a*) et la biomasse pélagique (1996–1998), l'ANOVA en mesures répétées montre un effet significatif du traitement et de l'année alors que seul le traitement est significatif pour la Chl *a* benthique (1997–1998). La concentration du Chl *a* augmente de 1,4 à 3 fois dans les lacs perturbés par rapport aux lacs de référence. Dans les lacs perturbés, la Chl *a* pélagique par unité de surface (milligrammes par mètre carré) est plus faible que la Chl *a* benthique. La communauté pélagique est dominée par les nanoflagellés mixotrophes dans les lacs de référence. Cependant, les perturbations du bassin versant induisent des changements différentiels dans la communauté d'algues pélagiques : les nanoflagellés mixotrophes augmentent dans les lacs de coupes alors que ce sont les diatomées phototrophes qui augmentent lors d'un feu. Lorsque l'on considère uniquement les lacs perturbés, la biomasse des algues est proportionnelle à la fraction du bassin versant perturbé divisée par la surface des lacs dans ce bassin.

Introduction

Aquatic ecosystems and wetlands occupy almost a third of the boreal ecoregion. More than 600 000 lakes larger than 4 ha are found in the Canadian Shield boreal region, south of 52°N latitude and east of the Manitoba–Ontario border (Minns et al. 1992). Timber harvesting in the Canadian boreal forest has increased in the last two decades and concerns have been raised over its potential impact on aquatic ecosystems. In the province of Québec, approximately 1% of the boreal forest is harvested annually (Ministère Ressources Naturelles Québec 1996).

The disturbances expected after logging are an increase in the watershed export of suspended solids, base cations, nutrients, and dissolved organic C (DOC) (e.g., Nicolson et al. 1982; Rask et al. 1998). In the boreal forest, similar disturbances in watershed exports occur naturally, mainly following wildfires, which also increase flow, silt loads, and chemical concentrations in waters (Bayley et al. 1992). As a consequence of these perturbations, nutrients may increase and light penetration may decrease, thereby modifying the water quality and productivity of impacted watersheds (e. g., Wright 1976; Carignan et al. 2000).

Studies on the effects of forestry practices are more common on running waters than on lakes (e.g., see Holopainen

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and Huttunen 1992). The few previous studies on the consequences of forest harvesting on lakes have only considered the response of pelagic organisms (Rask et al. 1998). However, benthic algal communities can be responsible for a significant fraction of the primary production in lakes, either in shallow systems or in deep oligotrophic lakes, and their importance in whole-lake metabolism is often neglected (Loeb et al. 1983; Wetzel 1996). Furthermore, the littoral zone is the main feeding area of many freshwater fish species.

The objectives of this study were to analyse changes in biomass and community structure of phytoplankton in boreal eastern Canadian Shield lakes disturbed by fire and harvesting and to compare the responses of pelagic and littoral algae with these disturbances.

Material and methods

The study area (~50 000 km^2) is centered on Gouin Reservoir (47°52′–48°59′N, 73°19′–76°43′W) (Fig. 1) at the transition zone between the boreal mixed and the boreal conifer forest (see Carignan et al. 2000). Thirty-two thermally stratified lakes were selected on the basis of several criteria (Carignan et al. 2000). Initially, the experimental design consisted of 16 lakes located within unperturbed watersheds, defined as a watershed untouched by fire or anthropogenic influences for a minimum of 40 years and, in general, for more than 70 years (reference lakes, N in Fig. 1). Of the harvested lakes, seven had approximately 9–73% of their watershed logged in 1995 (C in Fig. 1) and one was harvested twice, once in 1995, and once in 1997 (C9 in Fig. 1). Nine lakes had 50–100% of their watershed area severely burnt in 1995 (burnt lakes, FP and FBP in Fig. 1).

Sampling

Phytoplankton were sampled three times per year, in spring (within 2 weeks of ice-out), summer, and fall, from 1996 to 1998. Duplicate integrated samples from the euphotic zone (depth of 1% light penetration, between 2 and 5 m) were taken near the deepest part of the lake. Benthic algae were sampled using artificial substrates (70-µm Teflon® mesh; D. Planas et al., unpublished data) in reference lakes (four for the summers of 1997 and 1998 and six for winter), burnt lakes (five in 1997 and 1998), and cut lakes (four for the summers of 1997 and 1998 and six for winter). We used artificial substrates to minimize the heterogeneity of communities and to facilitate comparisons between systems. Benthic biomass as chlorophyll *a* (Chl *a*) was measured at two to four stations per lake on quadruplicate substrates placed at a depth of 1 m and left in the field for 3 months during the summers of 1997 and 1998 (summer benthic algae) and during 9 months from September 1998 to May 1999 (winter benthic algae).

Phytoplankton and benthic algal biomass measurements

Water samples for pelagic algae were transported to the laboratory on ice and Chl *a* was concentrated within 12 h by filtering a known amount of water (750–1000 mL) on Whatman GF/C filters. The filters were immediately frozen and kept at −40°C until extraction. Phytoplankton Chl *a* was extracted using hot 90% ethanol and absorbance was measured spectrophotometrically, before and after acidification (Sartory and Grobbelaar 1984). For measurements of benthic algal Chl *a*, the Teflon® substrates were transported to the laboratory on ice and kept frozen at −40°C until analysis. Chl *a* was extracted directly from artificial substrates by immersing them in hot 95% ethanol for 5 min.

A portion of the pelagic sample was preserved with acid Lugol solution for taxonomic analyses. Algae were identified, measured, and counted with an inverted interferential microscope. Phytoplankton counts were converted to wet weight biomass (biomass) using average species dimensions (mean of 40 cells) and corresponding geometric shapes and assuming a specific density of 1 (Lewis 1976). Species were assigned to one of three fractions according to the longest cell dimension: picoplankton, <2 µm; nanoplankton, 2–20 µm; microplankton, >20 µm.

Data analyses

In order to compare the relative importance of pelagic and benthic algae, phytoplankton biomass per unit volume was transformed to unit area of photic zone as phytoplankton biomass (milligrams per cubic metre) × photic zone depth (metres). The benthic to pelagic biomass ratio was estimated as average benthic biomass per lake (milligrams per square metre) × littoral area (square metres)/average phytoplankton biomass per lake (milligrams per square metre) × area of the pelagic euphotic zone (square metres). The littoral area was defined as the surface area of bottom sediments receiving more than 1% of the light extinction coefficient (ε_{PAR}). For benthic algae, we assumed that the biomass at 1 m corresponded to maximum biomass, since the substrates were at a fixed depth in all lakes. This coarse approach probably underestimated benthic algal Chl *a*, since typical epilithic algal profiles in oligotrophic Shield lakes show maximum Chl *a* concentrations below the 10% surface incident light depth (D. Planas et al., unpublished data), and artificial substrates after a 3-month colonization period have, in general, lower algal biomass than natural substrates (D. Planas et al., unpublished data). We could not exclude the possibility that our calculations overestimated benthic algal biomass, since factors other than depth and irradiance also regulate littoral algal biomass in lakes.

Statistical analyses were performed on $\log_{10}$-transformed data when necessary using SAS 6.14 and JMP 3.2.5 statistical packages (SAS institute Inc., Cary, N.C.). For pelagic Chl *a* and biomass and for summer benthic Chl *a*, univariate repeated-measures ANOVA (RMA) were applied to examine changes in Chl *a* and biomass measurements over time (1996, 1997, and 1998 for pelagic algae and 1997 and 1998 for benthic algae) for each treatment (reference, burnt, and harvested). One-way ANOVA was performed on wintering benthic Chl *a* (1998–1999). When an effect was significant, a Dunnett one-tailed *t* test was applied to compare reference and treated lakes. Differences among treatments and among years were tested using Tukey's honestly significant difference test for multiple comparisons. The *t* tests were used for benthic data (two years sampled) and for pelagic and benthic comparisons.

Multiple regressions were performed with a stepwise variable selection ($p < 0.05$ as an entering and keeping level) using Mallow's Cp as a model selection criterion, and colinearity between variables was accounted for by using a variance inflation factor. Normality of the predicted–observed residuals was verified with a Shapiro-Wilk *W* test. Correlations between phytoplankton taxon and physical and chemical variables were calculated using the Pearson product-moment pairwise method. Finally, we used ANCOVA (covariance on intercept and heterogeneity of slopes for regression coefficients) to test if the regression relationships between Chl *a* and total P (TP) (data from Carignan et al. 2000) and the ratio of Chl *a* to TP and ε_{PAR} (data from Carignan et al. 2000) were different among groups of perturbed lakes.

Results

Response of pelagic algal biomass

RMA on pelagic Chl *a* and biomass concentrations showed significant effects between treatments (burnt and harvested lakes with more than 10% catchment perturbed) and years (within treatments). The interaction term was significant for Chl *a*, indicating that temporal changes are de-

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Fig. 1. Location of the 32 study lakes in the Haute-Mauricie (Québec). N, reference lakes; FP and FBP, burnt lakes; C, harvested lakes (cut in 1995). The circles mark the lakes in which benthic algae were sampled.

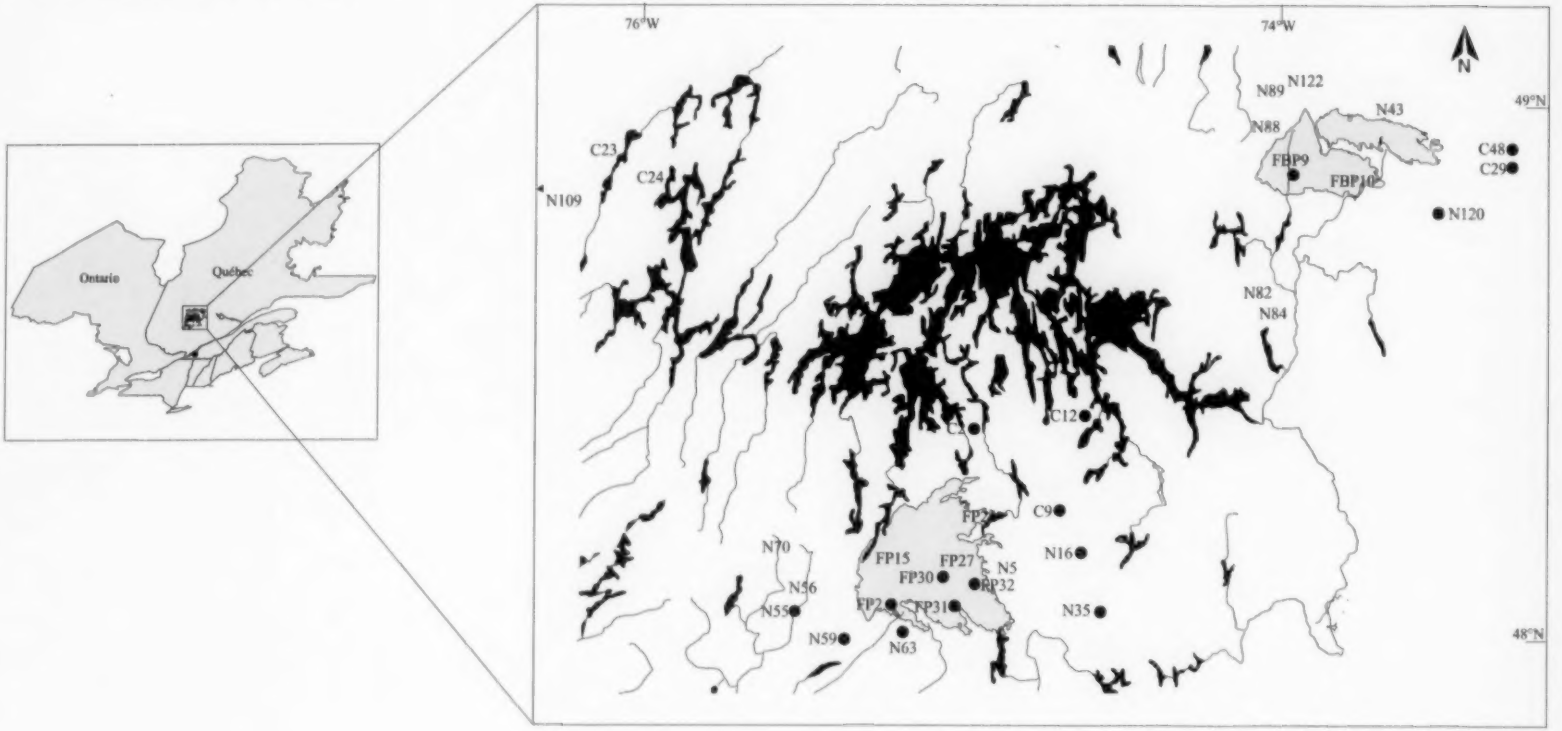

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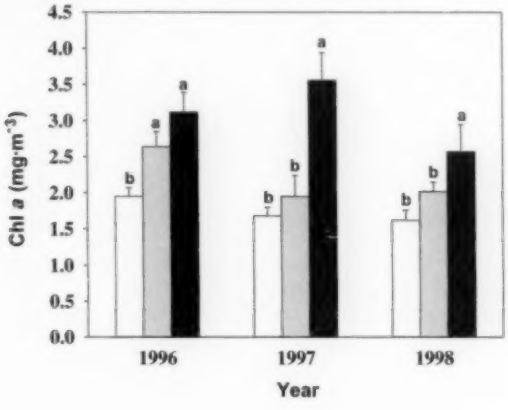
Table 1. Results of univariate RMA for phytoplankton Chl *a* ($mg \cdot m^{-3}$), wet weight biomass ($mg \cdot m^{-3}$), and summer benthic Chl *a* ($mg \cdot m^{-2}$, 3-month colonization) and one-way ANOVA for winter benthic Chl *a* ($mg \cdot m^{-2}$, 9-month colonization).

	Type III SS	df	*F*	$p > F$
Phytoplankton Chl *a*				
Treatments	0.48	2	13.33	0.0001
Years	0.07	2	11.01	0.0001
Treatments × years	0.06	4	4.77	0.0022
Wet weight biomass				
Treatments	2.36	2	17.08	0.0001
Years	0.33	2	10.9	0.0001
Treatments × years	0.11	4	1.83	0.1384
Summer benthic Chl *a*				
Treatments	0.72	2	6.25	0.0174
Years	0.04	1	0.04	0.1119
Treatments × years	0.02	2	0.02	0.5636
Winter benthic Chl *a*				
Treatments	2.44	112	18.36	<0.0001

Fig. 2. Average summer means ± SE of pelagic algal Chl *a* for reference (open bars, $n = 16$), harvested (grey bars, $n = 7$), and burnt lakes (black bars, $n = 9$). Different letters indicate mean differences ($p < 0.05$, ANOVA) within sets of lakes.



pendent on lake watershed treatment (Table 1). Over the 3-year period, perturbed lakes had higher mean Chl *a* and biomass than reference lakes ($p < 0.05$, Dunnett's test) (Figs. 2 and 3). Regardless of treatment, 1996 had higher Chl *a* and biomass than 1998 ($p < 0.05$, Tukey's test) and values in 1997 were intermediate ($p > 0.05$) between 1996 and 1998. A comparison within years found higher Chl *a* and biomass in perturbed lakes as compared with reference lakes in 1996 ($p < 0.05$), and these differences persisted only in burnt lakes for 1997 and 1998. Burnt lakes had higher Chl *a* in 1997 than in 1998 ($p < 0.05$, Tukey's test).

A highly significant relationship ($r^2 = 0.69$, $p < 0.0001$) was found between pelagic algal Chl *a* and biomass when data for all years and treatments were combined. However, when regressions were performed by treatment, the strongest relationship was found in burnt lakes ($r^2 = 0.66$, $p < 0.0001$) and the weakest in harvested lakes ($r^2 = 0.40$, $p < 0.002$).

Fig. 3. Annual average total biomass of pelagic algae taxa. R, reference lakes ($n = 16$); H, harvested lakes ($n = 7$); B, burnt lakes ($n = 9$).

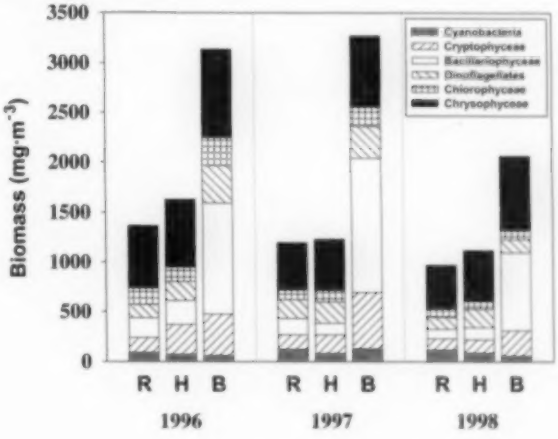
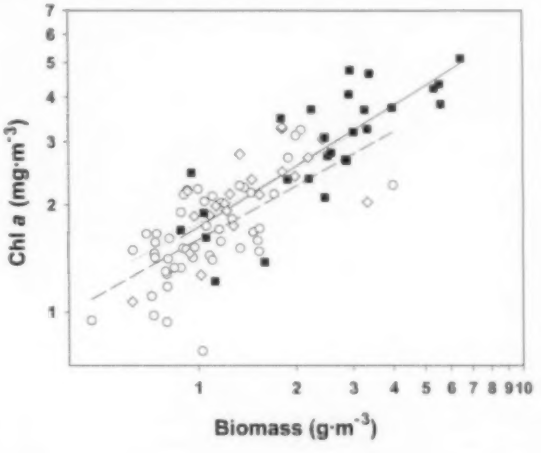


Fig. 4. Regression plot between pelagic algal Chl *a* concentrations and pelagic algal biomass (wet weight) for reference lakes (circles), harvested lakes (diamonds), and burnt lakes (squares) (log(Chl *a*) = –0.745±0.085 + 0.389±0.027log(biomass); $r^2 = 0.69$, $p < 0.0001$, $n = 96$). The dotted line, dashed line, and solid line indicate the linear fit for reference, harvested, and burnt lakes, respectively.



The relationship was also weak in reference lakes ($r^2 = 0.42$, $p < 0.0001$) (Fig. 4). ANCOVA indicated nonsignificant differences between slopes ($p > 0.05$) and intercepts ($p > 0.05$) among treatments.

Phytoplankton communities were dominated by the nanoplankton fraction, which represented between 76 and 91% of the total biomass. Nanoplankton increased in burnt and harvested lakes 1 year after perturbation and, in comparison with reference and harvested lakes, remained high 2 and 3 years after perturbation in burnt lakes ($p < 0.05$). In harvested and reference lakes, nanoplankton biomass tended to decrease from 1996 to 1997 ($p < 0.05$). Picoplankton biomass represented between 3 and 13% of the total biomass

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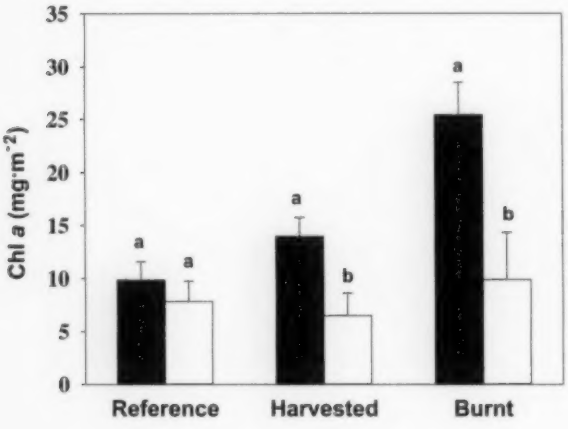
Fig. 5. Average summer means ± SE of benthic algal (solid bars) and pelagic algal (open bars) Chl *a* concentrations per unit area in reference and perturbed lakes. Different letters indicate mean differences ($p < 0.05$; *t* test) within sets of lakes.



and was higher in reference than in harvested and burnt lakes ($p < 0.05$). In reference lakes, picoplankton increased between 1996 and 1998 ($p < 0.05$). Microplankton biomass represented between 8 and 18% of the total biomass increase in harvested lakes in 1997 and was higher than in reference and burnt lakes ($p < 0.05$).

The dominant communities in the nanoplankton fractions were Chrysophyceae and Cryptophyta taxa. This association is characteristic of oligotrophic boreal lakes (Kling and Holgrem 1972; Willén et al. 1990). Cyanobacteria communities, the most important taxa within the picoplankton fraction, were dominated by small chroococcales, which were abundant in terms of numbers but of minor importance when converted to biomass. Cyanobacteria species found in our study are typical of temperate, nutrient-poor, dark waters and are abundant in eastern Canadian Shield lakes in the middle of summer, often associated with small green chlorococcales (D. Planas et al., unpublished data). Harvesting barely changed the phytoplankton community composition in lakes; some taxa increased, such as Chrysophyceae, Cryptophyceae, and dinoflagellates, or decreased, as was the case for cyanobacteria. More drastic changes in community composition were measured in burnt lakes 1 year after perturbation; diatoms became the dominant taxa and Cryptophyceae also increased in these perturbed lakes (Fig. 3).

Response of benthic algal biomass

In the littoral zone, algal communities also had higher Chl *a* in perturbed lakes compared with reference lakes. RMA on benthic summer Chl *a* showed only significant treatment effects (Table 1). Among perturbed lakes, burnt lakes had the highest concentrations of Chl *a* ($p = 0.0025$) (Fig. 5). For both years, Chl *a* concentrations were threefold higher in burnt lakes than in reference lakes, and in 1997, burnt lakes had twofold higher Chl *a* concentrations than harvested lakes (data not shown). A one-way ANOVA on wintering benthic algae also showed differences among treatments ($p < 0.0001$) (Table 1). Mean wintering algal Chl *a* concentrations in lakes impacted by harvesting (23.30 $mg \cdot m^{-2}$) and wildfire (29.06 $mg \cdot m^{-2}$) were higher than in reference lakes (14.57 $mg \cdot m^{-2}$), but the difference between harvested and burnt lakes was not significant ($p < 0.05$, Tukey's test) (Table 1). In 1998, mean Chl *a* concentrations in the littoral zone were higher in winter than in summer, for any treatment (reference, $p = 0.0008$; harvested, $p = 0.0001$; burnt, $p = 0.0014$; *t* test).

Biomass budget

In the subset of 16 lakes for which littoral algae were sampled, the comparison of littoral versus pelagic algal biomass (Chl *a*) per unit area of photic zone was estimated from the average summer biomass of 1997 and 1998 combined. When both communities were compared, differences were only found in perturbed lakes in which littoral Chl *a* was higher than pelagic Chl *a* (Fig. 5). The means of the ratios of benthic to pelagic algal biomass were 1.31 in reference lakes, 2.56 in harvested lakes, and 2.74 in burnt lakes (Fig. 5).

Physical and chemical variables influencing algal Chl *a*

Pelagic algal Chl *a* could be predicted by TP, which explained 48% of the partial variance, followed by ε_{PAR} and dissolved inorganic N (DIN = $NO_3 + NO_2 + NH_4$) (data from Carignan et al. 2000), which explained 6 and 4% of the variance, respectively (Table 2). The same variables entered into the biomass regression model, but the predictive power in this model was slightly weaker for TP, but not for ε_{PAR} and DIN, than contribute slightly more to the total variance (Table 2). The relationship between TP and Chl *a* in perturbed lakes is shown in Fig. 6A, and for the same set of lakes, the relationship between the ratio of Chl *a* to TP and ε_{PAR} is shown in Fig. 6B.

Catchment characteristics as well as the area of cut or burnt watershed that predicted the physical and chemical water changes in our lakes (Carignan et al. 1999), also predicted changes in pelagic biomass (Fig. 7). For phytoplankton biomass, the fraction of the watershed perturbed over the sum of lake surface areas in the watershed explained 57% of the variance in Chl *a*.

TP was the best predictor of benthic algal Chl *a* concentrations in summer, explaining 34% of the variance, followed by NO_3 and DOC, which accounted for 17 and 11% of the variance, respectively (Table 2). TP as well as DOC also showed a relationship with winter benthic algal Chl *a*, but total N (TN) explained a stronger percentage of the variance (Table 2).

Variables influencing algal taxon composition

In general, correlations between phytoplankton taxon composition and environmental variables were significant, although correlation coefficients were low. Cryptophyta and Bacillariophyceae (diatoms) showed weak positive correlations with TP ($r^2 = 0.29$, $p = 0.0038$ and $r^2 = 0.34$, $p = 0.0007$, respectively). Bacillariophyta was also correlated with DIN ($r^2 = 0.5070$, $p < 0.0001$) and Cryptophyta with ε_{PAR} ($r^2 = 0.3998$, $p = 0.0001$). Chrysophyceae, cyanobacteria, and Chlorophyceae showed weakly negative rela-

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Table 2. Multiple or simple regression models of yearly averages of algal biomass and physical and chemical variables of lakes (independent variables): (*a*) phytoplankton Chl *a*, (*b*) phytoplankton wet weight biomass, (*c*) summer benthic algal Chl *a*, and (*d–f*) winter benthic algal Chl *a*.

(*a*) $\log_{10}$(Chl *a*) = –0.168±0.061 + 0.700±0.090log(TP) – 0.322±0.113log(ε_{PAR}) + 0.074±0.022log(DIN)				
	$r^2_{partial}$	0.48	0.06	0.04
SSE = 0.75	$r^2_{adjusted}$ = 0.565	F = 42.1	$p < 0.0001$	n = 96
(*b*) $\log_{10}$(biomass *a*) = 1.951±0.139 + 1.270±0.204log(TP) – 0.925±0.255log(ε_{PAR}) + 0.220±0.053log(DIN)				
	$r^2_{partial}$	0.31	0.10	0.07
SSE = 2.85	$r^2_{adjusted}$ = 0.489	F = 31.3	$p < 0.0001$	n = 96
(*c*) $\log_{10}$(Chl *a*) = –0.414±0.320 + 0.650±0.320log(TP) + 0.169±0.068log(NO_3) + 0.847±0.517log(DOC)				
	$r^2_{partial}$	0.34	0.17	0.11
SSE = 0.62	$r^2_{adjusted}$ = 0.568	F = 11.9	$p < 0.0001$	n = 26
(*d*) $\log_{10}$(Chl *a*) = –0.109±0.288 + 1.320±0.275log(TP)				
SSE = 0.16	r^2 = 0.622		p = 0.0003	n = 16
(*e*) $\log_{10}$(Chl *a*) = –3.414±0.856 + 1.931±0.353log(TN)				
SSE = 0.15	r^2 = 0.681		$p < 0.0001$	n = 16
(*f*) $\log_{10}$(Chl *a*) = 0.095±0.225 + 1.407±0.303log(DOC)				
SSE = 0.16	r^2 = 0.606		p = 0.0004	n = 16

Note: Physical and chemical data from Carignan et al. (2000). $p = p > F$; biomass is wet weight; ε_{PAR} is the available radiation light extinction coefficient.

tionships with nutrients, including both TP (r^2 = –0.20, p = 0.0472, r^2 = –0.42, $p < 0.0001$, and r^2 = –0.22, p = 0.0289, respectively) and DIN (r^2 = –0.39, p = 0.0001, r^2 = –0.21, p = 0.0417, and r^2 = –0.22, p = 0.0344, respectively). The negative correlations of these taxa with water column nutrients suggests that they were not directly controlled by nutrients.

Discussion

Algal responses to watershed perturbations

Phytoplankton biomass (Chl *a* and biomass) as well as the dominant taxa in the reference lakes of our study region were characteristic of pristine oligotrophic Canadian Shield lakes (Armstrong and Schindler 1971; Kling and Holgrem 1972). Within perturbed watersheds, and particularly in burnt lakes, volumetric biomass increased to mesotrophic levels (Chl $a > 3$ mg·m^{-3}, biomass > 3000 mg wet weight·m^{-3}) with maximum Chl *a* concentrations greater than 5 mg·m^{-3}. Moreover, increases in taxa such as diatoms, which are more characteristic of boreal enriched environments (Eloranta 1986), only occurred in burnt lakes. Benthic algal biomass responses to watershed perturbations followed the same pattern as for phytoplankton; the response was, however, magnified relative to the pelagic community, particularly in burnt lakes. In burnt lakes, benthic algal Chl *a* as high as 100 mg·m^{-2} was measured 2 years after perturbation, while in references lakes, the highest Chl *a* measured was approximately 30 mg·m^{-2}. Other studies have also reported considerable increases in benthic algal biomass following boreal forest disturbance ranging from 21- to 46-fold in rivers and from two to fourfold in lakes compared with reference systems (Holopainen and Huttunen 1992; Rask et al. 1998). In our study, benthic algal Chl *a* in the perturbed lakes was only two to three times higher than in the reference lakes and is thus comparable with boreal lake responses (Rask et al. 1998).

Even 3 years after perturbations, algal communities in the lakes may not have reached a steady state. Long-term responses to disturbances have been reported in aquatic ecosystems following watershed perturbations, such as wildfires (Wright 1976; Minshall et al. 1997). During our 3-year study, the greatest response was measured in the second year following disturbances, and the sign of the response was different in relation to the type of disturbance. Biomass increased and major taxa shifts were observed in burnt lakes, whereas biomass decreased in harvested lakes. These interannual differential changes in algal biomass and (or) species composition in lakes with perturbed watersheds could be explained by variability in chemical fluxes and light penetration. Higher runoff was measured in 1997 compared with 1996 and 1998 in the region of the Gouin Reservoir (Lamontagne et al. 2000). Nutrient loading was equivalent in both types of perturbations for 1996 and 1998, and it was 50% higher than in reference lakes. The increase in P loading in 1997 was 25% higher in burnt lakes than in harvested lakes (S. Lamontagne, GRIL, Université de Montréal, C.P. 6128, Montreal, QC H3C 3J7, Canada, personal communication). However, the large difference in chemical loading between harvested and burnt lakes was a result of the large increase in DOC (50–80%) in harvested watersheds, which was not observed in burnt watersheds (S. Lamontagne, GRIL, Université de Montréal, C.P. 6128, Montreal, QC H3C 3J7, Canada, personal communication). Higher DOC concentrations in harvested lakes strongly influenced light penetration in our study lakes (Carignan et al. 2000). Thus, low light transmission could explain, for any year, the small response of algal biomass in harvested lakes as compared with burnt lakes, and this in spite of similar nutrient loadings. Moreover, light differences between treatments could

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Fig. 6. (A) Relationship between 3-year average pelagic algal Chl *a* in perturbed lakes (harvested (diamonds) and burnt (squares)) and TP ($\log(\text{Chl } a) = -0.407\pm0.233 + 0.789\pm0.224\log(\text{TP})$; $r^2 = 0.47$, $F = 12.38$, $p > F = 0.0034$, $n = 16$). (B) Relationship between the Chl *a*/TP ratio in perturbed lakes and ε_{PAR} ($\text{Chl } a/\text{TP} = 0.135\pm0.014 - 0.107\pm0.036\log(\varepsilon_{PAR})$; $r^2 = 0.38$, $F = 8.60$, $p > F = 0.0109$, $n = 16$).

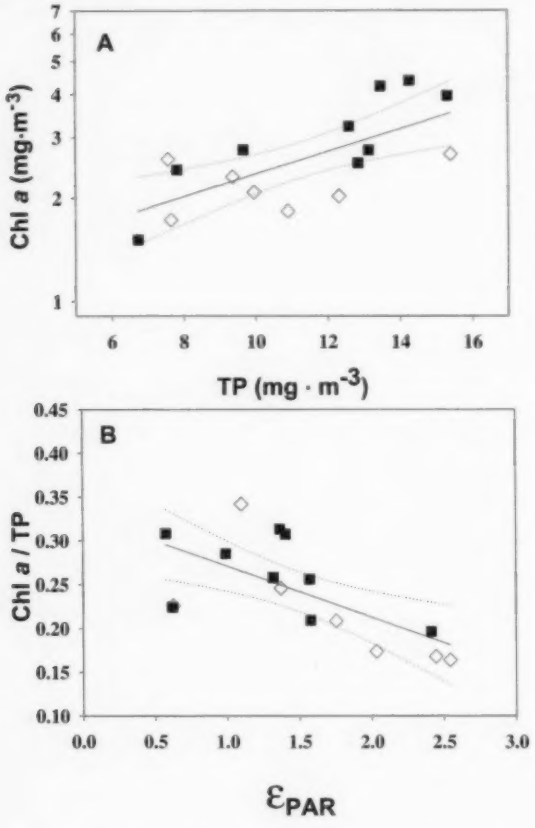
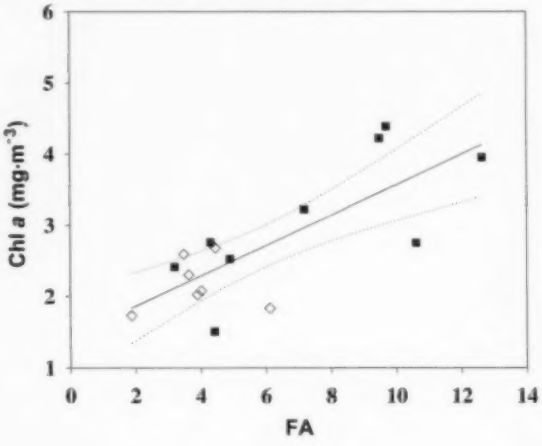


Fig. 7. Relationship (solid line) and 95% confidence intervals (dotted lines) between phytoplankton Chl *a* in perturbed lakes (harvested (diamonds) and burnt (squares)) and the fraction of the watershed perturbed over the sum of lake surface areas in the watershed (FA) ($\log(\text{Chl } a) = 0.412\pm0.036 + 0.024\pm0.006\text{FA}$; $r^2 = 0.570$, $F = 18.53$, $p > F = 0.0007$, $n = 16$).



explain the lack of difference in pelagic algal Chl *a* per unit area between treatments. Low light, when nutrients are available, could limit algal primary production and hence biomass (Petersen et al. 1997). For a similar increase in nutrients in perturbed lakes, differences in ε_{PAR} could also explain differences in the algal taxa responses, which are discussed below.

Relationship between algal responses and physical and chemical lake characteristics

TP was the best predictor of pelagic algal biomass in the study lakes. For a given P concentration, lakes in burnt watersheds produced more Chl *a* per unit TP than harvested lakes. It is well known that P limits phytoplankton production in boreal Canadian Shield lakes (Schindler 1974) and, as mentioned before, watershed perturbation in our study increased TP export by twofold as compared with references lakes (Lamontagne et al. 2000). Nitrogen also seemed to have had some control on pelagic algal biomass responses. It is known that N plus P additions yielded the greatest biomass response as compared with additions of one or the other alone (Axler et al. 1994). Thus, in our burnt lakes, increases in P and N loading increased algal biomass per unit volume. Harvesting increased TP concentration but not inorganic N concentrations (Carignan et al. 2000), and thus, lower N could explain the lower algal biomass in harvested lakes as compared with burnt lakes. However, lower light penetration could also explain the lower Chl *a* concentrations per unit biomass in harvested lakes in relation to burnt lakes.

The fact than N showed stronger relationships with benthic rather than pelagic algal Chl *a* could be explained by the differences in nutrient availability in the littoral as compared with the pelagic zones. Phosphorus release from littoral epilimnetic sediments could support benthic algal growth, while pelagic algae rely on P dissolved in the water column (Carlton and Wetzel 1988). While the export of N increased in both harvested and burnt watersheds, N was primarily exported as NO_3 in burnt lakes and probably as dissolved organic N in harvested lakes (Lamontagne et al. 2000). Higher NO_3 fluxes into the lakes could thereby help to explain the higher algal benthic biomass in burnt lakes. The positive relationship between DOC and benthic algae biomass seen in our study suggests that DOC could enhance littoral algal growth, as was observed in an experimental study by Vinebrooke and Leavitt (1998). In our lakes, DOC regulates underwater spectral irradiance, but we do not know if it also influences lake chemistry. DOC can complex metals and enzymes that regulate P availability (Boavida and Wetzel 1998) or, conversely, can act as a source of labile organic substrates, such as P and dissolved inorganic C (Moran and Zepp 1997). DOC is also a vector for nutrients such as N and P (Lamontagne et al. 2000). Although in our study, we did not determine the proportion of nutrients that enter the lake in the dissolved organic form, it is possible that in boreal catchments, it is the more important form of nutrients (Lamontagne et al. 2000). In our multiple regressions, P ex-

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plained a greater percentage of benthic algal biomass in summer as compared with winter. The wintering algae were exposed to spring runoff, which contributes a high percentage of the annual runoff in our lakes, as, in general, in temperate regions (Likens 1985). Thus, in spring, when UV radiation is higher than in late summer, photolysis of DOC could reactivate the alkaline phosphatase binding with humic substances, thereby promoting P availability for littoral algae (Boavida and Wetzel 1998).

It has been observed that catchment variables can explain the variability of Chl *a* almost as well as that of TP (Duarte and Kalff 1989). In our study lakes, some of the easily measured catchment characteristics, such as the area of cut or burnt watershed, predict the physical and chemical changes in our lakes (Carignan et al. 1999) as well as changes in pelagic biomass. The highest Chl *a* concentrations occurred in burnt lakes ($p = 0.001$, t test), particularly in the FP region where the 1995 wildfire hit more severely the lake's shoreline. This relationship allowed for the prediction of either lake water quality or the response of primary producers and could be a useful tool for managers.

Changes in pelagic algal community associated with environmental variables

Moderate enrichments, such as those observed in the perturbed lakes, may also explain increases or changes in algal community taxa (Eloranta 1986; Willén et al. 1990). Diatom increases in burnt lakes could be expected as a result of P and, to a lesser extent, N augmentations in these lakes (Jansson et al. 1996; Watson et al. 1997). Cryptophyta and Chrysophyceae also increased in perturbed lakes, but these increases cannot be explained by nutrients with which the biomass of these two taxa were weakly or negatively correlated. Weak correlations of these taxa or curvilinear responses with TP increases have been reported and attributed to morphological diversity, differential herbivory, and mixing regime (Watson et al. 1997). In our study, the relatively strong correlation of nutrients with diatoms and the weak or absent relationship of nutrients with Cryptophyta and Chrysophyceae cannot be explained by differential grazing or mixing. Thus, in all taxa, the species present in our lakes were edible, and no strong relationship was found between phytoplankton and herbivorous zooplankton (Patoine et al. 2000), and the thermal characteristics of these lakes did not differ (Carignan et al. 2000).

Dominance of Cryptophyta and Chrysophyceae, representing almost 90% of the biomass, has been found in boreal brown-water lakes (Kling and Holgrem 1972; Willén et al. 1990), and Cryptophyceae increases have been measured in brooks of harvested watersheds (Holopainen and Huttunen 1992; Lepistö and Saura 1998). In our study, the negative relationship between nutrients and Chrysophyceae and light penetration and Cryptophyta suggests that the species present in our lakes are capable of obtaining their energy via means other than photoautotrophy, e.g., phagotrophy, heterotrophy, or photoheterotrophy (Pick and Caron 1987). In Canadian Shield lakes, stronger phagotrophic particle uptake has been demonstrated in some Chrysophyceae species, and phagocytosis was the dominant path for energy flow when photosynthesis was light limited (Bird and Kalff 1987). Mixotrophy has also been reported in Cryptophyta (Tranvik et al. 1989). Thus, the different responses of taxa observed in our study in relation to the type of perturbation, namely the increase in photoautotrophic algae in burnt lakes but not in harvested lakes, may be associated with differences in light penetration.

Biomass budget

The littoral versus pelagic biomass (Chl *a*) per unit of surface area indicated a stronger response of littoral communities to pertubations. Since no other studies investigating the impact of watershed disturbance on lakes have simultaneously measured the response of pelagic and benthic algae, no comparisons with the literature were possible. However, it is known that in humic oligotrophic lakes, phytoplankton and benthic algae compete for nutrients (Hansson 1990). Nutrient loading in the littoral zone is less diluted than in the pelagic water column, and the efficiency of nutrient utilization, retention, and recycling is much greater among closely aggregated benthic algal–microbial communities than in the pelagic zone (Wetzel 1996). These littoral characteristics lead to maximal resource utilization and productivity per areal unit. In nine perturbed lakes, in which benthic algal biomass was measured, nutrients in the water column were relatively abundant compared with unperturbed lakes, suggesting that competition for nutrients between littoral and pelagic zones was weaker in relation to reference lakes. However, due to differences in the concentration of DOC, the amount of light reaching the substrates differed between treatments (Carignan et al. 2000), with 25% of surface irradiance (ε_{PAR}) in reference lakes, 14% in harvested lakes, and 10% in burnt lakes. Low light penetration in perturbed lakes could increase the Chl *a* content of cells (Ahlgren 1970), but mean Chl *a* per algal cell in phytoplankton was equal in reference and harvested lakes. For benthic algae, however, Chl *a* per unit cell was higher in burnt lakes ($p < 0.05$) than in harvested or reference lakes (D. Planas et al., unpublished data). Consequently, we cannot exclude the possibility that higher Chl *a* concentrations in benthic algae in burnt lakes are related to lower light conditions as compared with reference lakes. For the burnt lakes in which benthic algae were studied, the 1997 and 1998 mean euphotic zone to mixing depth ratio (Z_{ph}/Z_{mix}) was lower than 1 ($Z_{ph}/Z_{mix} = 0.796 \pm 0.106$) and less ($p < 0.05$) than in the reference lakes ($Z_{ph}/Z_{mix} = 1.31 \pm 0.101$), while it was intermediate in harvested lakes ($Z_{ph}/Z_{mix} = 0.992 \pm 0.106$).

In conclusion, increases in nutrient loading as a consequence of watershed perturbation may modify algal biomass and induce changes in the pelagic algal community structure. The littoral algae showed a greater response to perturbations than pelagic algae. Responses were somewhat different for lakes on harvested watersheds as compared with lakes in burnt watersheds. Lack of riparian vegetation in some burnt watersheds may explain why biomass and algal composition responses were greater in burnt lakes than in harvested lakes. Three years after perturbation, algal biomass may still have not reached a steady state. At present, results indicate that TP is the main nutrient driving these changes, although total pelagic productivity in the perturbed lakes could be impaired by low light penetration. Changes in species composition among perturbed lakes did not induce the development of inedible algae in the pelagic zone. How-

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ever, because N seems to play some role and if N export decreases through time and P continues to leach from the watershed, we can expect the development of toxic cyanobacteria. Decreases in biomass associated with light limitation or changes in algal quality due to changes in N/P ratios could negatively affect fish communities in these pristine boreal lakes. Although we could not discount the influence of natural interannual variability on our results because preperturbation data from these lakes were not available, our study does indicate that simple empirical models incorporating perturbation scenarios and variables such as lake area, which is easily measured from maps, could be used in the development of sustainable harvesting practices.

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Paleolimnological reconstruction of forest fire induced changes in lake biogeochemistry (Lac Francis, Abitibi, Quebec, Canada)[1]

Mihaela Enache and Yves T. Prairie

Abstract: Biogeochemical effects of fire events were analysed in a small humic kettle lake, Lac Francis (claybelt area, Abitibi, northwestern Quebec), using diatom-based quantitative inference models developed to reconstruct past pH, total phosphorus, and dissolved organic carbon in Abitibi lakes. Diatom-inferred changes in lake geochemistry in four historical fire events were examined and the results showed that, on average, total phosphorus concentrations increased significantly (up to twofold) during fire events. In contrast, dissolved organic carbon concentrations and pH were relatively unaffected by the fires.

Résumé : Les effets des feux de forêt sur la biogéochimie du Lac Francis, un petit lac humique de la ceinture argileuse d'Abitibi (nord-est du Québec), ont été analysés en utilisant des modèles quantitatifs d'inférence développés pour la reconstruction du pH, du phosphore total et du carbone organique dissous dans les lacs Abitibiens. Les changements dans la biogéchimie inférés par les diatomées ont été examinés sur quatre feux de forêts historiques et les résultats montrent, qu'en moyenne, le phosphore total augmente significativement (jusqu'à deux fois) durant les événements de feux. Par contre, les concentrations de carbone organique dissous et le pH sont peu affectés.

Introduction

Because of its ecological importance, forest fire is one of the most documented natural disturbances of the boreal forest (e.g., Bergeron 1991; Dansereau and Bergeron 1993; Liski et al. 1998). Forest fires radically affect the structure and the dynamics of the boreal forest and act as a reset mechanism for the successional sequence. The boreal forest is a fire-adapted biome, where fire and fire-prone species promote each other in a feedback loop that reaches different equilibrium points in different climatic and physical settings (Campbell and Flannigan 1998). Many factors influence the occurrence and the frequency of forest fires: climate (temperature, precipitation, wind), geographical location, forest type, and quantity and quality of fuel. While many authors maintain that the present and forecasted global climate changes will increase forest fire frequency (e.g., Beer and Williams 1995; Schindler et al. 1996), others maintain that, in certain areas (notably in the Abitibi region, northwestern Quebec), fire frequency is likely to decrease (Bergeron and Archambault 1993).

Lakes are an integral part of the boreal landscape, and in the Abitibi region, they occupy about 6% of the surface area (Y.T. Prairie, unpublished data). If forest fires affect the structure and composition of the forest, the chemistry and hydrology of the watersheds and the lakes into which they drain are obviously perturbed as well. Burning increases surface runoff and erosion by reducing evapotranspiration and by destroying the surface litter layer and possibly by exposing the mineral soil to rainfall (Shahlaee et al. 1991). It can also reduce infiltration by creating hydrophobic conditions causing yet more surface runoff and more erosion (De Bano 1981). Danielovich (1986), however, found that forest fires in upstate South Carolina had little impact on infiltration, erosion, or soil exposure. While several authors (e.g., McColl and Grigal 1975; Wright 1976; Bayley et al. 1992) reported increased nutrient and base cation export from burned catchments, others (e.g., Lewis 1974; Richter and Ralston 1982) argued that no important changes take place in the litter and in the hydrologic fluxes of nutrients, sulfur, and base cations from burned areas. These results, at times contradictory, reflect the complexity of the processes induced by forest fires on the watershed area and the modulating influence of regional conditions. In northwestern Ontario, fires contributed to increased wind velocities, larger surface waves, greater transparency, and deepening of the thermocline (Schindler et al. 1996). Nevertheless, it is clear that the topographic setting, geological substrate, forest composition, and fuel properties, as well as the local climate circumstances, can affect the responses of watersheds and lakes to fires (Schindler et al. 1980). It is therefore difficult to predict what effect fires will have on lakes draining specific catchments.

Due to the inherent unpredictability of the location of forest fires and their long cycle (as long as 300 years or more in parts of eastern Canada; Green 1982), it is very difficult to directly assess the variability in the geochemical response of

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Fig. 1. Geographical location of Lac Francis. The shaded area is the catchment delimitation.

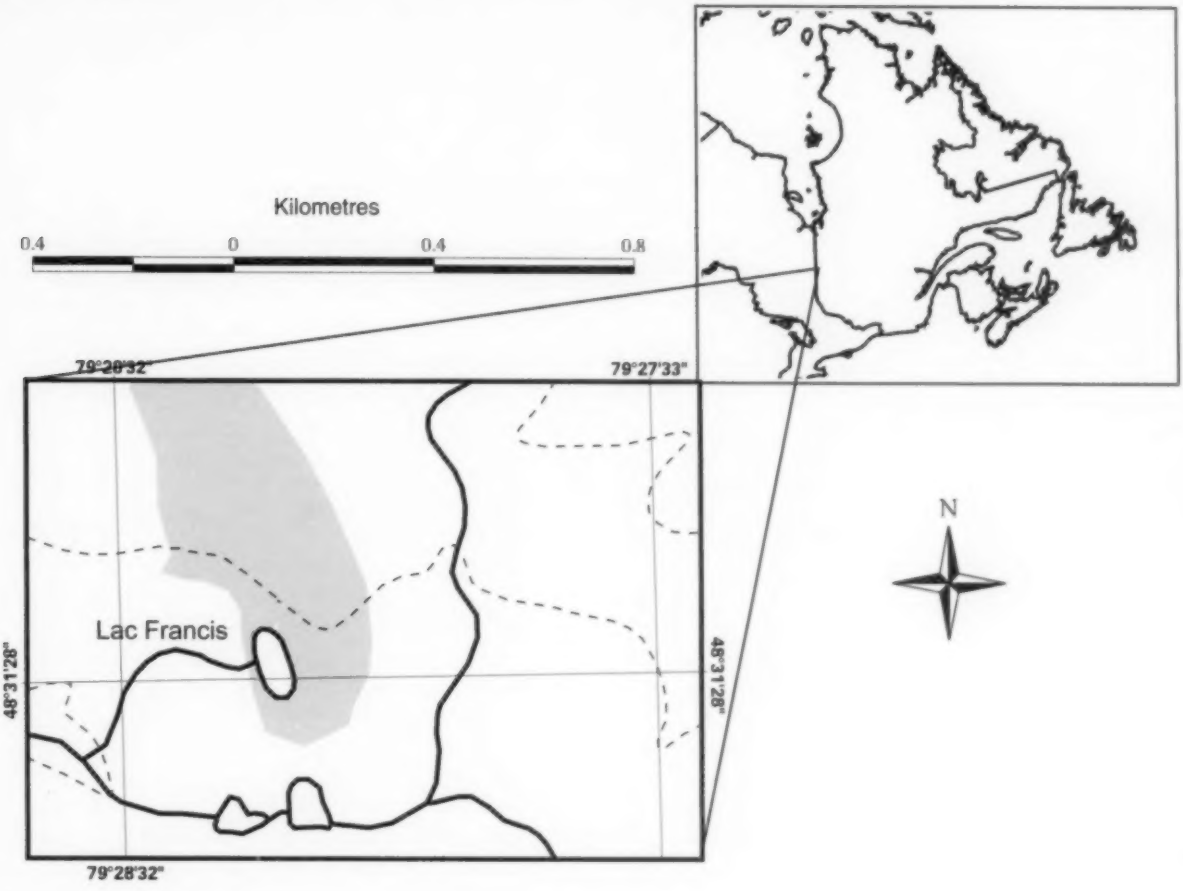

Table 1. Morphometric and physicochemical characteristics of Lac Francis.

Variable/parameter	Value
Coordinates	48°32′N, 79°28′W
Lake area (km^2)	0.01
Watershed area (km^2)	0.21
Watershed slope (%)	0.03
Maximum depth (m)	6.0
Secchi depth (m)	0.8
pH	5.5
TP ($\mu g \cdot L^{-1}$)	27.5
TDP ($\mu g \cdot L^{-1}$)	8.0
TN ($\mu g \cdot L^{-1}$)	565
TDN ($\mu g \cdot L^{-1}$)	382
DOC ($mg \cdot L^{-1}$)	14.5
NO_3 ($\mu g \cdot L^{-1}$)	1
NH_4 ($\mu g \cdot L^{-1}$)	12
Alkalinity ($\mu equiv \cdot L^{-1}$)	71
Chlorophyll *a* ($\mu g \cdot L^{-1}$)	33

lakes to forest fires. The only long-term investigations possible require the use of paleolimnological tools, which have been only rarely applied to examine the effects of forest fires on lake biogeochemistry (Rhodes and Davis 1995; Korhola et al. 1996; Paterson et al. 2000). Both Rhodes and Davis (1995) and Korhola et al. (1996) reported an increase of about 1 pH unit after the fire. On the other hand, Paterson et al. (2000) showed that limnological changes following forest fire were not evident in chrysophyte assemblages and hypothesized that climate may have exerted an overriding influence on lakes during the studied period (i.e., 1970–1990).

In another work (Enache and Prairie 2000), we have developed, from a calibration set of 42 lakes from the Abitibi region, weighted averaging partial least squares (WA-PLS) transfer functions to estimate pH, total phosphorus (TP), and dissolved organic carbon (DOC) based on diatom assemblages. The aim of the present paper is to use these transfer functions to reconstruct both the fire history and the associated changes in lake geochemistry in a small kettle lake, Lac Francis.

Materials and methods

Study site

Lac Francis is a small humic kettle lake of about 1 ha sur-

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Table 2. Summary of diatom-based WA-PLS inference models and their RMSEP, R^2, and the number of associated PLS components.

	pH	TP ($\mu g \cdot L^{-1}$)	DOC ($mg \cdot L^{-1}$)
RMSEP	0.25	3.25	2.57
R^2	0.93	0.8	0.64
No. of PLS components	3	3	2

rounded in part by a floating bog (Fig. 1). It is situated at 305 m above sea level in northwest Abitibi, 15 km south of Lake Abitibi. Its theoretical water residence time is estimated at about 4 months. The area was covered by the proglacial Lake Ojibway for about 2000 years until it drained into the Tyrrell Sea about 8000–9000 years ago (Richard 1980;Veillette 1994). The present topography of the region alternates between flat clay plains and steep hills (Morin et al. 1992). Overlying basalts, Lac Francis is a quasi-confined acidic pond developing an anoxic hypolimnion with at present no inflowing streams and therefore very little exogenous inputs other than direct precipitation and groundwater inputs. The lake is known to contain discontinuously varved sediments (C. Carcaillet et al., Department of Forest Vegetation Ecology, Swedish University of Agricultural Sciences (SLU), S-901 83 Umeå, Sweden, unpublished data). Because of these characteristics, Lac Francis is an ideal lake for testing the effects of fire disturbances in its catchment during its historical past. More detailed morphometric and physicochemical characteristics of Lac Francis are given in Table 1.

Sampling

A 2.98-m sediment core was collected in April 1996 from the deepest point of the lake using a Livingstone corer. Upon extrusion, the core was found to be laminated with some discontinuities, particularly in the upper portion of the core. The central core was cut into contiguous 1-cm slices; three 1-cm^3 subsamples for microcharcoal, pollen, and diatom analysis were taken from each slice. The residual sediment was used for plant macrofossil analysis and radiocarbon dating (C. Carcaillet et al., Department of Forest Vegetation Ecology, Swedish University of Agricultural Sciences (SLU), S-901 83 Umeå, Sweden, unpublished data).

Microcharcoal analysis and chronology

The surface area of microcharcoal on pollen slides was measured under a microscope using a grid with 400 squares of 156 μm^2 of surface area at 400× magnification. Estimated dates of fires were derived from 10 (AMS) ^{14}C dates. The ^{14}C measurements were calibrated to dendrochronological years using the CALIB 3.0 program (Stuiver and Reimer 1993). The details of the chronology in relation to the laminations were discussed by C. Carcaillet et al. (Department of Forest Vegetation Ecology, Swedish University of Agricultural Sciences (SLU), S-901 83 Umeå, Sweden, unpublished data).

Preparation of diatom samples

Preparation of diatom samples followed standard methods (Battarbee 1973, 1986) used for sediment samples without $CaCO_3$. An aliquot (0.2 mL) was added with 1 mL of exogen contaminant (*Eucalyptus globulus*) solution and resuspended in distilled water (5–10 mL final volume). An aliquot (0.2 mL) of this resulting mixture was evaporated onto coverslips and mounted onto glass slides with Naphrax (IR = 1.65).

Identification and counting of diatom taxa

For each sample, a minimum of 400 diatom valves were identified and counted under oil immersion objectives at 1000–1600× magnification along random transects. Transects include a peripheral area, and only valves including an identifiable central area were counted. For each fire event, we analysed the abundance and relative frequency of diatom taxa at two levels before and after the level with the microcharcoal peak representing the fire event.

Diatom taxonomy follows standard flora (Hustedt 1930–1966; Germain 1981; Camburn et al. 1984–1986 Krammer and Lange-Bertalot 1986–1991). Diatom taxa were identified to the lowest taxonomic level (i.e., variety).

Numerical analyses

Transfer functions were established using a 42-lake training set from the Abitibi area covering a wide geochemical range. The details of these transfer functions are discussed in Enache and Prairie (2000) but are briefly summarized here. First, we determined whether linear or unimodal-based numerical methods were appropriate for our data on the basis of a detrended correspondence analysis with detrending by segments (Legendre and Legendre 1998). If the gradient length is 2 SD units or more, unimodal-based ordination methods were deemed appropriate (Birks 1995). In our case, a detrended correspondence analysis of 164 diatom taxa and measured environmental variables revealed gradient length greater than 2 SD units. To identify environmental variables that were highly correlated, we proceeded to a Bonferroni-corrected correlation matrix and a principal components analysis. Environmental variables that are highly correlated are TP with total dissolved phosphorus (TDP), pH with alkalinity, and total nitrogen (TN) with total dissolved nitrogen (TDN). Many canonical correspondence analyses with the environmental variable as the sole predictive variable were done to eliminate outlier samples that had very high chi-square distances and absolute residuals (observed–predicted) greater than the standard deviation of the environmental variable of interest. Only one lake (Lac KI) was removed from the training set as an outlier because its extreme value in TP (52.0 $\mu g \cdot L^{-1}$). Finally, a canonical correspondence analysis with seven selected environmental variables (pH, TN, NH_4, NO_3, TP, DOC, Secchi depth) and 164 diatom taxa using the forward selection and the associated Monte Carlo test revealed that the variables that explain statistically significant ($p \leq 0.05$) parts of the variance in diatom taxa are pH, TP, and DOC. Next, WA-PLS models (sensu Ter Braak and Juggins 1993) that were statistically significant ($p \leq 0.05$) were used to reconstruct past lake water pH, TP, and DOC. Species with tolerances of more than 2 pH units, 9 $\mu g \cdot L^{-1}$ in TP concentration, and 3 $mg \cdot L^{-1}$ in DOC concentration were automatically excluded in quantitative reconstruction. The apparent root mean square error of prediction (RMSEP) of each inference model was evaluated with a cross-validation (leave-one-out jackknifing) procedure (Table 2). Numerical analyses were computed using the statistical program CANOCO 3.12 (Ter Braak 1988, 1990) and a SAS/IML implementation of WA-PLS (Y.T. Prairie, unpublished data).

Results and discussion

The sedimentary microcharcoal concentration profile of Lac Francis showed clear peaks that we attributed to fire events close to the lake (Fig. 2). We considered that a fire event likely occurred within the lake's catchment when the level containing the microcharcoal peak was more than 1.2 times greater than the smoothed background (C. Carcaillet et al., Department of Forest Vegetation Ecology, Swedish University of Agricultural Sciences (SLU), S-901 83 Umeå, Sweden, unpublished data) and was well delimited from preceding levels and when microcharcoal of large size-classes was present within the sample (Clark 1988). Similar patterns were identified when the microcharcoal data were expressed as an accumulation rate (data not shown) rather than concentration. Although we believe that our approach reasonably

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Fig. 2. Microcharcoal concentration and lamination structure along the sedimentary profile of Lac Francis.

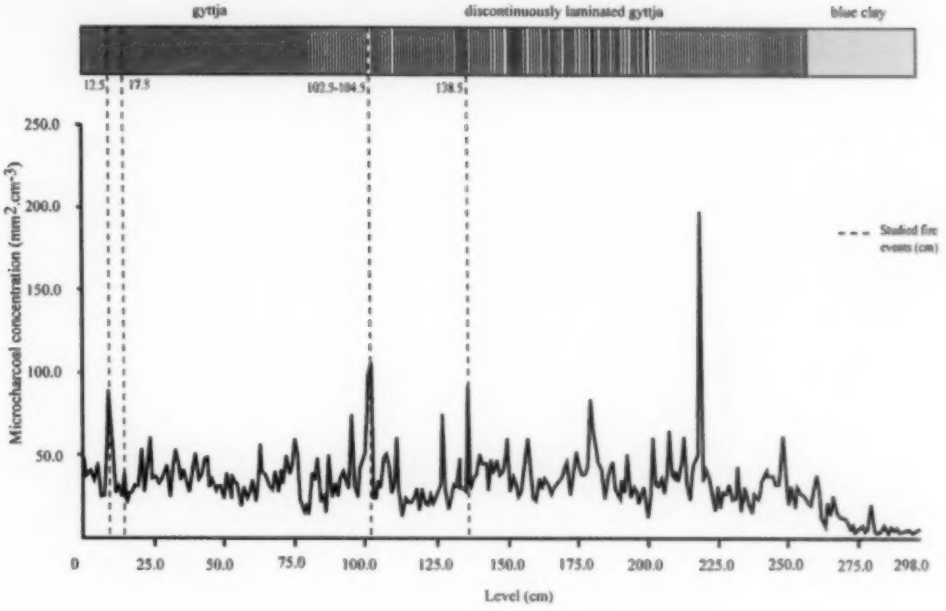

Table 3. Stratigraphical distribution of studied fire events and their characteristics: age (^{14}C years BP cal), years since previous fire (years cal) without fire events, and charcoal concentration index (current/background microcharcoal concentration ratio).

Level (cm)	Age	Years since previous fire	Charcoal index
12.5	186±80	56	1.9
17.5	242±80	69	1.29
102.5–104.5	1448–1466±70	169	1.55–1.7
138.5	2165±120	429	2.08

ensures that the fires are local, this is clearly a limitation of the paleolimnological approach as applied to fires.

Some microcharcoal peak levels (e.g., 220.5 and 209.5 cm) were eliminated because of their nearly inexistent diatom flora. The 17.5-cm fire event showed only a small microcharcoal index (1.29). Based on the ^{14}C chronology, this peak corresponds to the historically confirmed fire of 1760 (Bergeron and Harvey 1997), and we therefore retained this fire in our analysis. In all, we studied four fire events within the core, the oldest dating from over 2000 years ago (Table 3). The selection of the fire events used in the diatomological analysis was essentially arbitrary but purposely included both recent and old fires.

Changes in the diatom assemblages and fire events

The oldest studied fire event occurs at a depth of 138.5 cm (2165 years BP cal), about 400 years after the last preceding fire event. It occurred during the latter part of a warm and humid climate period with long fire intervals (Bergeron et al. 1996). The diatom assemblages of the prefire levels are characterized by very low abundances (Fig. 3) and high species richness (about 66 species in the 140.5-cm level and 50 species in the 139.5-cm level) dominated by *Pinnularia braunii* (23.41–29.43%). Most other species have low relative frequencies (*Brachyssira brebissonii*, *Eunotia bilunaris*, *Eunotia pectinalis*, *Fragilaria brevistriata*) (Fig. 3). The disturbance level coincided with a highly increased diatom abundance (double prefire levels) (Fig. 4), an important diminution in species richness (about 20 species), and drastic changes in the specific composition of diatom taxa. For example, *Aulacoseira distans tenella* and *Aulacoseira distans humilis* became very abundant (Fig. 3). *Pinnularia braunii* remained abundant within the fire level and many species became either absent (e.g., *B. brebissonii*, *E. bilunaris*, *E. pectinalis*, *Frustulia rhomboides*, *Gomphonema gracille*, *Gomphonema parvulum*) or rare (*Cymbella gaeumanii*, *Tabellaria ventricosa*). In the postfire levels (137.5, 136.5, and 135.5 cm), *A. distans tenella* and *A. distans humilis* remained high in relative abundance, but we noted a decrease in *A. distans tenella* frequency, while *P. braunii* increased its relative frequency to 62.3%. The next fire event occurred within the 102.5- to 104.5-cm level (1448–1446 years BP cal). The three levels all have high microcharcoal concentrations (Fig. 4) with relatively abundant plant macrofossils. The laminations in the sediment profile within these levels were highly irregular or absent. We thus interpreted these three successive high microcharcoal concentration levels as a single highly smoothed fire event.

As in the preceding case, prefire levels (105.5 and 106.5 cm) are characterized by low diatom abundance. The assemblages are broadly dominated by *P. braunii* and *A. distans humilis* (Fig. 3), two low nutrient concentration and acidic–circumneutral related taxa (Whitmore 1989). The fire levels present drastic changes in diatom assemblages: a significant increase in absolute abundance (Fig. 4), an decrease in *P. braunii*, and an increase in *A. distans humilis* frequency within the 104.5-cm level, while within the 103.5-

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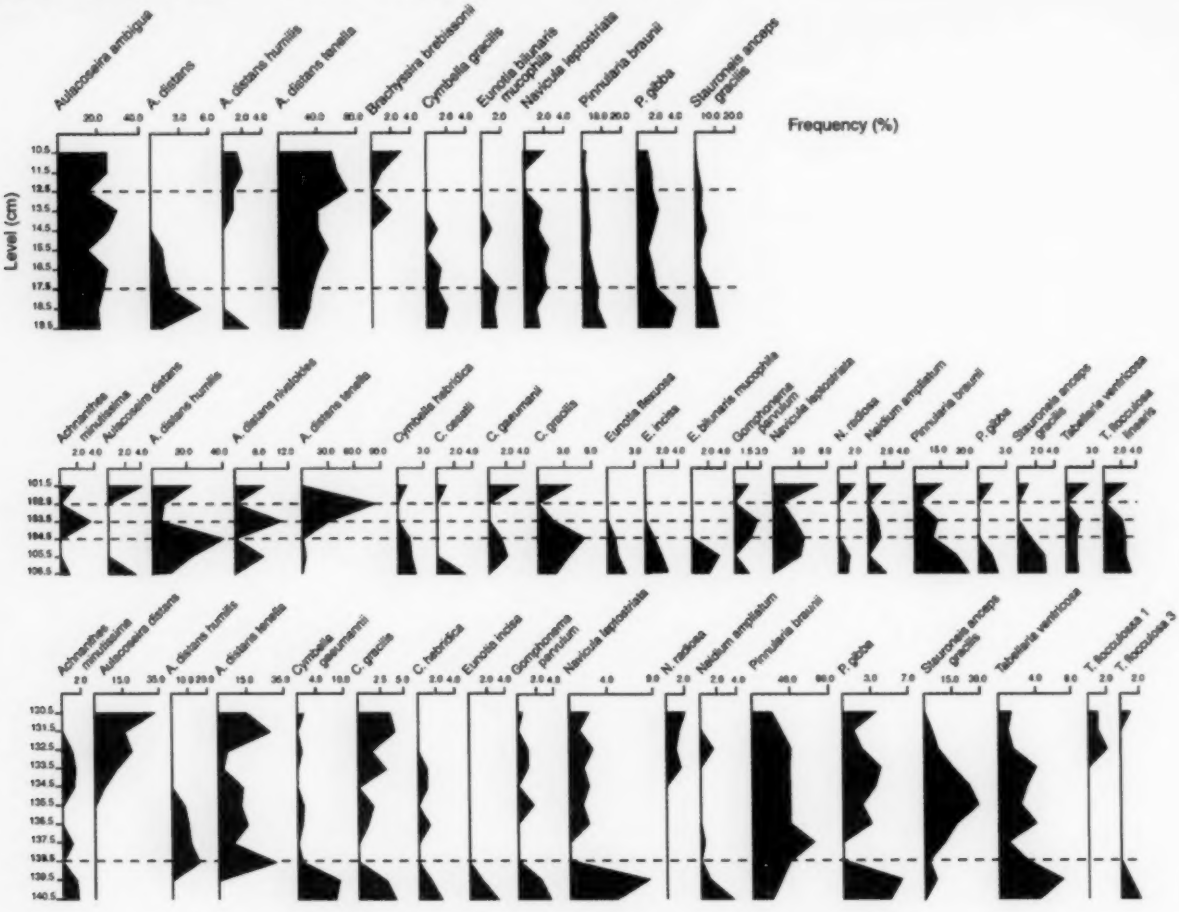
Fig. 3. Stratigraphical distribution of selected taxa among the studied intervals.



cm level, we noted the presence of *Aulacoseira distans nivaloides*, the diminution of *A. distans humilis*, and an increase in *P. braunii* among the most frequent species. However, the most important change in diatom assemblages occurs within the 102.5-cm level (Figs. 3 and 4). Absolute diatom abundance increased by more than three times and is largely attributable to a bloom of *A. distans tenella*. All other species disappeared or were present at very low percentages. Species richness increased (*A. distans humilis*, *P. braunii*, *A. distans nivaloides*, *C. gracilis*, *T. ventricosa*) within the postfire 101.5-cm level, while absolute abundance decreased dramatically (Fig. 4). The two most recent fire events (17.5 and 12.5 cm) had a less important impact on the diatom assemblages than the older events studied. The species composition did not vary substantially (*Aulacoseira ambigua* and *A. distans tenella* remained the most frequent taxa) between prefire, within, and postfire levels. Only small changes in relative frequencies were observed.

Impact of fires on diatom-inferred lake geochemistry

TP

Fluctuations in diatom abundance and species composition generally reflect changes in environmental factors. Diatom-inferred TP values revealed important chemical changes in the fire or postfire levels. As with the total diatom abundance, the most important changes were detected in the oldest fires studied (138.5- and 102.5- to 104.5-cm levels). Diatom-inferred TP revealed important increases in TP concentrations within these fire disturbance levels. Relative to prefire concentrations, diatom-inferred TP values increased by about 4 and 13 $\mu g \cdot L^{-1}$, respectively (Fig. 4). In the most recent fire events (17.5 and 12.5 cm, or 186 and 242 years BP cal, respectively), WA-PLS inferred values showed some increase in TP concentrations but less important than in the preceding cases (Fig. 4). To compare the relative impact of forest fires on TP concentrations among the four studied fires, we calculated the ratio between fire (and postfire) values and the mean of the prefire values. The results, illustrated in Fig. 5, show that there is a highly significant difference between prefire and fire values ($p < 0.01$) and between fire and postfire values ($p < 0.01$) but that the difference between prefire and postfire values is not statistically significant ($p > 0.05$). There was a strong impact of fire at the 138.5- and 102.5- to 104.5-cm levels on lake water TP concentrations, with increases of 55 and 150% relative to prefire

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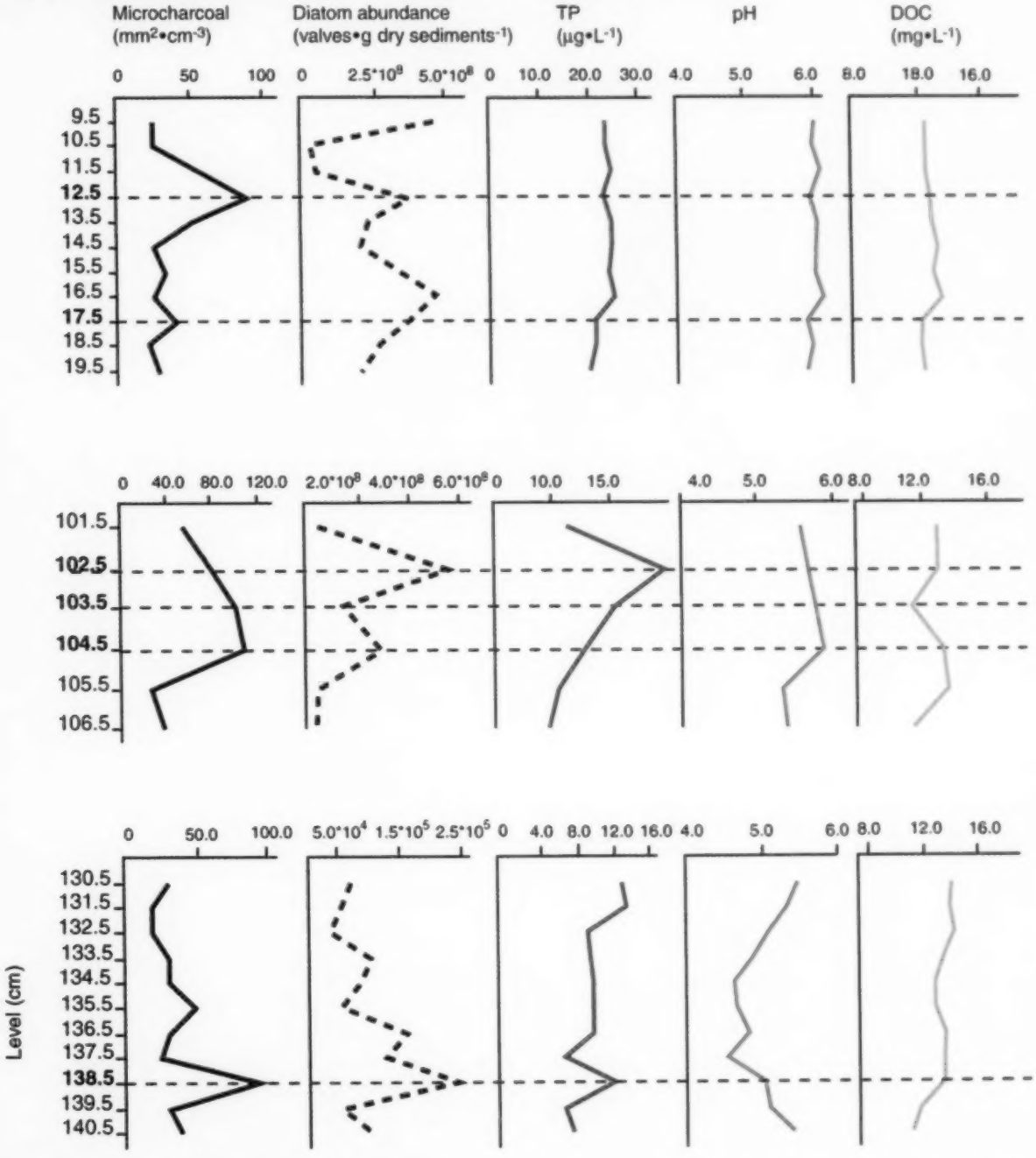
Fig. 4. Microcharcoal concentration, diatom absolute abundance, and diatom-based WA-PLS inferred values of TP, pH, and DOC among the studied stratigraphical intervals. Horizontal broken lines indicate fire levels.



concentrations, respectively. In contrast, the more recent fires (corresponding to 17.5 and 12.5 cm) had much lower or no detectable impact on TP concentrations, with maximum increases of only 20 and 1%, respectively. Thus, while fires have an overall effect on lake TP concentrations (on average, an increase of 51%), the magnitude of the effect varies considerably from fire to fire. Several hypotheses can explain why the most recent fires apparently had a lesser effect on P concentrations than the older fires, but we consider the following as most plausible. First, Lac Francis is more eutrophic now than it was 2000 years ago. A time series of prefire diatom-inferred TP values over the last 2000 years

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Fig. 5. Average relative increase (relative to prefire diatom-inferred TP concentration) in prefire, fire, and postfire values of diatom-inferred TP concentrations among the studied levels. A value of 1 indicates average prefire TP concentration.

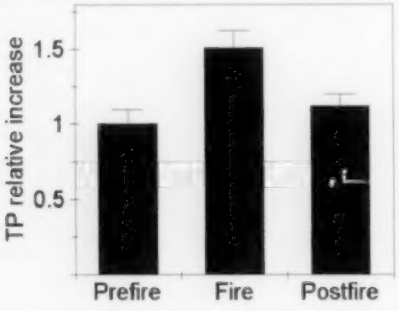
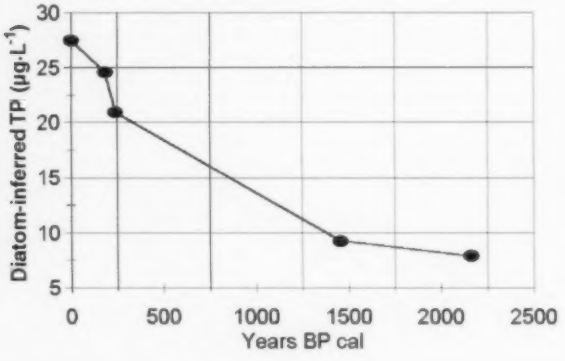


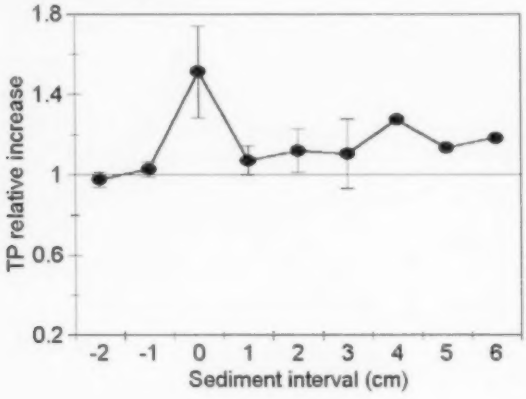
Fig. 6. Prefire diatom-inferred TP concentrations as a function of fire years BP cal. The value at 0 years BP cal is measured water column TP concentration in 1997.



shows that its P levels have increased more than threefold, from about 7–8 to about 25 $\mu g \cdot L^{-1}$ (Fig. 6). Additional nutrient inputs from a fire to an already eutrophic system may not be as readily detectable from diatoms, as they are in a prefire oligotrophic lake and as factors other than nutrients are more likely to limit diatom growth in eutrophic waters. A second hypothesis is that the two recent fires occurred within a moist and warm period with less favorable fire conditions (Bergeron et al. 1996) and with shorter fire cycles. Climate conditions in combination with maturity, thickness, and properties of the litter can produce more or less intense forest fires and consequently different impacts on lake biogeochemistry. Because of the more humid climate conditions and smaller fuel load (due to the short fire cycles (Table 3)), these fires may have been less intense. This would have lessened the evapotranspiration differential and reduced the availability of inorganic P generated by the less efficient burning of nutrient-rich plant matter, all of which would have contributed to lower nutrient export to lake.

Irrespective of the exact mechanisms involved, it is clear from Fig. 5 that the impact of fires on TP concentrations is relatively short-lived. While postfire values are on average 12% higher than prefire values, the difference was not statistically significant. The same conclusion was drawn when each sediment interval was treated separately and not

Fig. 7. Average relative increase (relative to prefire diatom-inferred TP concentration) in diatom-inferred TP concentrations for each 1-cm sediment interval (negative values are prefire intervals, 0 is the fire interval, and postive values are postfire intervals for all studied fire events. A value of 1 indicates average prefire TP concentration.



lumped into prefire, fire, and postfire categories (Fig. 7). Thus, the maximum temporal extent of the impact of fires does not significantly exceed the time frame covered by a 1-cm accumulation of sediment. In Lac Francis, depending on the particular fire considered, each 1-cm slice corresponds to between 13 and 16 years. This recovery period seems reasonable given the short water residence time of Lac Francis and the time needed for the forest cover to reestablish itself. It is likely, however, that the impact of forest fires on P concentration may be detectable for longer periods of time in slow-flushing lakes. Assuming constant P retention (as a fraction of inputs) within the lake, lake P concentration should be proportional to loading, suggesting a much greater export of P from the watershed in the few years following a fire. High nutrient (TP) inputs are probably the combined result of several factors such as the supply by the burnt soil organic matter and the disappearance of the vegetation cover, which leaves nutrients available for leaching from watershed to lake or directly from wind-blown ash. The reduced evapotranspiration should also increase the area of catchment saturated with water, thereby facilitating both exchange and transport of nutrients (D'Arcy and Carignan 1997). A comparison of estimated P loadings to lakes with recently burnt catchments and unperturbed systems also concluded that P loading increased by an average of about 50% and varied among catchments from no increase to a doubling relative to reference systems (Lamontagne et al. 2000). These results are strikingly similar to the variability seen within Lac Francis among fires. However, the reasons for this variability either among catchments or among fires within a catchment are not clear.

pH and DOC

Our diatom-based reconstruction of pH and DOC in Lac Francis showed little effect of fires on lake DOC and inconsistent effects on pH (Fig. 4). In the oldest fire studied, the pH was more acidic after the fire, while in the subsequent fire (102–104 cm), there was an apparent increase of about

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0.5 pH unit. Overall, however, we did not find any significant difference between prefire, fire, and postfires values ($p > 0.05$) for either pH or DOC. Similar results were obtained by Carignan et al. (2000) in their comparison of lakes within recently burnt catchments with unperturbed systems in the Haute-Mauricie region of Quebec (about 200 km east of Lac Francis). These results contrast with those of Rhodes and Davis (1995) and Korhola et al. (1996) who inferred higher pH resulting from fires, presumably due to the input of alkaline ashes. We suggest that possible alkaline inputs may have been counterbalanced by the much higher losses from the watersheds (with sulfates and nitrates as the main balancing anions) following fires (Lamontagne et al. 2000). It is also possible that the fire impact on pH and DOC concentration is significant but that it is much more short-lived than the impact on P and therefore less readily detectable from sediment slices pooling several years.

In conclusion, our diatom-based quantitative reconstructions of pH, TP, and DOC demonstrate the complexity of the response of boreal ecosystems to forest fires. Fire events are correlated with large increases in absolute diatom abundance and significant changes in the specific composition and (or) the relative frequency of diatom taxa. In contrast with many other studies, our results indicate that in the Abitibi region, forest fires can contribute, at least temporary, to the enrichment (TP) of lake waters. On the other hand, pH and DOC exhibited little change after fire events. Fire effects varied in magnitude among the studied intervals. We suggest that both the trophic status of the lake prior to the perturbation and the length of the fire cycle are important modulators of its biogeochemical response.

Our results also have implications for forest management practices, in particular concerning the short- versus long-term effects of natural perturbations on lake conditions. They set a baseline against which anthropogenic perturbations can be compared. First, the fire effects on the nutrient status of lakes appear relatively short-lived. It would be important to assess and compare the duration of the impact of anthropogenic perturbations such as logging. Second, we showed that fires can double the P concentration of Lac Francis. If generally applicable, this provides a management rule such that logging be permitted only to the extent that its effects are not larger than those of natural perturbations. Lastly, if the initial chemical balance is important in determining the sensitivity and response of a particular lake to natural disturbances, it is likely to be reflected in the lake's response to other types of perturbations as well. These considerations should be taken into account in forest management decisions.

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Do logging and forest fires influence zooplankton biomass in Canadian Boreal Shield lakes?

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Abstract: Zooplankton biomass was assessed in 20 reference lakes, nine logged-watershed lakes, and nine burned-watershed lakes during three summers following watershed disturbances by logging or wildfires. Biomass of cladocerans, calanoids, cyclopoids, and rotifers was quantified in the 38 lakes for the first year following disturbances. Limnoplankton biomass in four size fractions was quantified during 3 years following disturbances. One year after disturbances, burned-watershed lakes supported 59% more biomass of the rotifer size fraction of limnoplankton (100–200 μm) than reference lakes, while logged-watershed lakes supported 43% less of calanoid biomass. Two years after disturbances, differences in limnoplankton biomass between burned-watershed lakes and reference lakes were more pronounced than during the first year, while logged-watershed lakes supported levels of limnoplankton biomass no different from those of reference lakes. Three years after disturbances, no significant variations could be detected among the three groups of lakes for any of the limnoplankton size fractions. The proportion of watershed area impacted by logging activities was on average less than half the proportion impacted by wildfires. Nonetheless, both types of disturbances seemed to have opposite effects on the zooplankton biomass during the first year, and the effects did not extend beyond 2 years.

Résumé : La biomasse du zooplancton a été mesurée dans 20 lacs aux bassins versants intacts, neuf lacs aux bassins versants déboisés par la coupe forestière (lacs C) et neuf lacs aux bassins versants brûlés par des feux de forêt naturels (lacs F), et ce, pendant les trois étés qui ont suivi les perturbations de bassins versants. Pendant la première année après perturbations, la biomasse de limnoplancton comprise entre 100 et 200 μm, composée principalement de rotifères, était en moyenne 59% plus élevée dans les lacs F que dans les lacs de référence, tandis que la biomasse des calanoïdes était 43% plus faible dans les lacs C. Pendant la deuxième année, les différences de biomasse de limnoplancton entre lacs F et lacs de référence étaient encore plus élevées comparées à la première année, tandis que les lacs C montraient des biomasses équivalentes à celles des lacs de référence. Pendant la troisième année, aucune différence de biomasse n'était détectable entre les trois groupes de lacs. Les effets des feux de forêt sur la biomasse du zooplancton semblent opposés à ceux des coupes forestières pendant la première année et ne se prolongent pas au-delà de la deuxième année.

Introduction

Wildfires and logging each remove about 10 000 km^2 of Canada's 4.5 × 10^6 km^2 forest each year (Forestry Canada 1991). New strategies in forest management are based on the assumption that emulating natural disturbances such as wildfires in logging practices will sustain boreal forest dynamics and biodiversity (Hunter 1993). Such strategies, however, were developed without considering aquatic ecosystems, even though water represents 8% of Canada's surface area. Comparing the impacts of wildfires and logging on lake water quality and biota is a necessary step towards developing forest management practices that take into account the global impacts of logging on the forest–lake ecosystem.

Stream concentrations of particulate organic matter, phosphorus, nitrogen, and ions can increase following forest fires (Bayley et al. 1992) and clear-cutting (Likens et al. 1970). Following watershed disturbance, the biomass of stream macroinvertebrate communities has been shown to increase in some cases (Burton and Ulrich 1994) but not in others (Minshall et al. 1997). In comparison with the number of studies on streams, little work has addressed the consequences of watershed disturbance on lake aquatic communities. In some cases, forest harvesting was associated with increases in chlorophyll *a* (Chl *a*) concentrations and primary production (Rask et al. 1993), moderate increases in cladoceran and copepod density (Rask et al. 1998), and decreases in catch and biomass per unit effort of brook trout (*Salvelinus fontinalis*) (Bérubé and Lévesque 1995). In other cases, differences between logged-watershed lakes and reference lakes in Chl *a*, total phosphorus (TP), total nitrogen (TN), and dissolved organic carbon (DOC) concentrations were undetectable (Lehmann 1994). Presently, confounding factors such as the type of disturbance (logging or fire), the time elapsed since the disturbance, and the extent of natural

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Table 1. Characteristics of the 38 lakes and their watersheds for the three groups of watershed treatment.

	Reference (n = 20)	Logged (n = 9)	Burned (n = 9)
Maximum depth (m)	12 (7–23)	14 (5–30)	17 (10–34)
Lake area (ha)	44 (14–81)	56 (18–231)	40 (17–64)
Drainage ratio (drainage area/lake area)	5.4 (2.3–15.4)	6.7 (2.0–13.2)	7.1 (2.5–11.6)
% watershed area disturbed	0 (0–1)	38 (7–73)	90 (50–100)
pH	6.3 (5.8–7.0)	6.1 (5.7–7.0)	6.3 (5.6–7.2)
TP ($\mu g \cdot L^{-1}$)	6.9 (4.5–11.8)	9.5 (5.4–17.3)	11.8 (5.6–17.3)
TN ($\mu g \cdot L^{-1}$)	213 (118–332)	252 (160–386)	310 (169–747)
Chl *a* ($\mu g \cdot L^{-1}$)	1.7 (0.8–3.4)	2.0 (1.0–3.3)	3.1 (1.2–5.2)
Planktivores (catch per unit effort)	38 (0.3–206)	26 (8–106)	36 (0.1–128)

Note: Means (ranges in parentheses) are based on 3 years of sampling for chemical variables (R. Carignan, Université de Montréal, Montréal, Qué., personal communication). Fish abundances were based on catches in 1996 and 1997 (P. Magnan, Université du Québec à Trois-Rivières, Trois-Rivières, Qué., personal communication).

variability render any statement on the differential impacts of logging and fires on lake biota questionable.

Zooplankton represent an essential component of lake biota: by grazing on the phytoplankton community, zooplankton can control algal biomass and size structure (Christoffersen et al. 1993), contribute to nutrient recycling (Lehman 1980), increase water transparency (Lampert et al. 1986), and increase mixing depth (Mazumder et al. 1990). Zooplankton biomass in Canadian Boreal Shield lakes is positively related to the concentration of TP and TN (Yan 1986). It is therefore likely, but yet unknown, that zooplankton biomass in logged- and burned-watershed lakes is somewhat higher than in undisturbed-watershed lakes.

The present study is the first to compare the effects of forest fires and logging on the biomass of zooplankton in Canadian Boreal Shield lakes. We present the results of 3 years of zooplankton sampling in 38 lakes of central Québec characterised by different watershed conditions: undisturbed, logged, and burned. We predict that zooplankton biomass will be higher in logged- and burned-watershed lakes than in undisturbed-watershed lakes.

Materials and methods

Study lakes and sampling design

The study was conducted in 38 boreal lakes located on the Canadian Shield in Québec, around the Gouin reservoir. Lakes were distributed in three groups representing different watershed conditions: undisturbed (20 reference lakes), logged (nine lakes), and burned (nine lakes). The logging and natural forest fires all occurred in 1995, about 1 year before the beginning of the study. Logged-watershed lakes had 7–73% of their watershed area clear-cut in 1995 and had 20-m buffer zones of unharvested vegetation surrounding the lakes. Burned-watershed lakes had 50–100% of their watershed burned by natural forest fires, also in 1995. Lakes were chosen on the basis of comparable lake and watershed morphometry among the three groups of lakes (Table 1). Details on bedrock geology, landscape features, climate, and vegetation are presented in Carignan et al. (2000). The lakes were sampled three times per year, in May–June, July, and September of 1996, 1997, and 1998. All were sampled within 5 days between 06:00 and 15:00.

Zooplankton sampling and biomass determination

Zooplankton were sampled at the deepest point of the lakes with a 53-μm-mesh cantilevering net (Filion et al. 1993) from 1 m above the sediment to the surface. Filtered water volume varied between 80 and 1200 L depending on lake depth. Zooplankton were narcotised in the field with carbonated water and preserved in 4% formaldehyde. In the laboratory, the samples were split into four equal fractions with a Folsom splitter; one quarter was used for taxonomic analysis (see details below), one was used for size fractionation and organic mass determination of limnoplankton (see details below), and the two residual quarters were kept for later studies and reference material.

Taxonomic analyses were performed on 10-mL subsamples of the 1996 samples. Zooplankton were identified to species by following the keys of Edmondson (1959), Brandlova et al. (1972), and Smith and Fernando (1978). Naupliar and copepodite stages of calanoids were distinguished from those of cyclopoids. To estimate specific biomass, we measured the size of the first 30 specimens of each crustacean (length) and rotifer (length and width) species. Mean size values were converted to dry biomass using the length–mass relationships developed by Malley et al. (1989). Specific dry mass values were summed to obtain the biomass of four taxonomic groups (cladocerans, calanoids, cyclopoids, and rotifers) and total zooplankton biomass. Zooplankton biomass was expressed as milligrams dry weight per cubic metre.

Size-fractionated limnoplankton measurements were performed on the 1996, 1997, and 1998 samples. Each sample was sieved through a sequential array of nets of decreasing mesh sizes, 500, 200, 100, and 50 μm, to obtain four size fractions: 50–100, 100–200, 200–500, and >500 μm. The material collected on each net was then back-washed and filtered onto precombusted GF/A (Whatman) glass fiber filters, dried at 40°C for 18 h, weighed, ashed at 500°C for 18 h, and weighed again. Limnoplankton organic mass for each size fraction was calculated as the difference between the two weight measurements and expressed as milligrams ash-free dry weight (AFDW) per cubic meter.

Species composition of limnoplankton size fractions was determined under 20× magnification prior to drying. The >500 μm size fraction was principally composed of *Holopedium gibberum* (47% on average of the dry mass of this size fraction), *Daphnia* spp. (21%), adult calanoids (16%), and adult cyclopoids (15%). Hence, in this paper, the >500 μm size fraction will be referred to as the crustacean size fraction. The 200–500 μm size fraction was generally composed of calanoid copepodites (43%), cyclopoid copepodites (32%), nauplii (12%), and bosminids (6%) and will be referred to as the copepodite size fraction. The 100–200 μm size fraction was mostly composed of nauplii, rotifers, and algae, while the 50–100 μm consisted of rotifers and algae. These will be referred to as the rotifer and algal size fractions, respectively.

Statistical analyses

To test if watershed condition was a significant source of variation in zooplankton or limnoplankton biomass for the entire ice-

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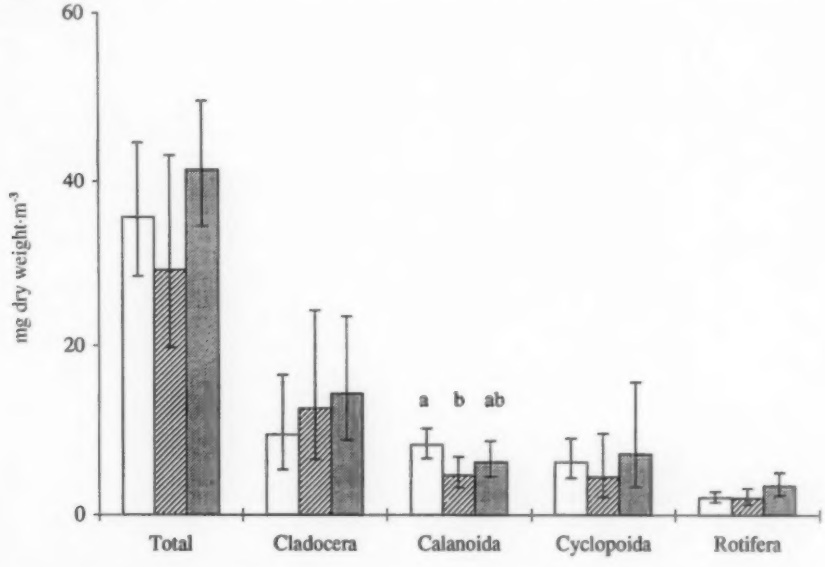
Fig. 1. Among-group differences in the 1996 average biomass of zooplankton taxonomic groups. Bars represent undisturbed- (open), logged- (hatched), and burned-watershed lakes (shaded). Error bars represent the 95% confidence intervals on the mean (back-calculated from log-transformed values). Bars with different letters represent groups with significantly different means (α = 5%, Scheffé's multiple range test).



free season, one-way repeated measures analyses of variance were performed for each zooplankton variable. The three samplings performed in each lake (June, July, and September) were treated as repeated measures. In the case of limnoplankton, a separate repeated measures analysis of variance was performed for each of the 3 years following watershed disturbance (1996, 1997, and 1998).

Where F tests revealed a significant treatment effect (α = 5%), the Scheffé multiple range test was performed to assess where differences lay (SAS Institute Inc. 1988). Where F values were declared nonsignificant, a power analysis was performed to quantify the risk of type II error (Cohen 1988). Analyses of variance were also performed for each sampling period separately to determine when among-group differences in biomass were strongest.

To examine if zooplankton biomass was related to disturbance intensity (percentage of watershed area logged or burned) independently of disturbance type (logging or fire), regression analyses were performed between the different variables of zooplankton biomass (dependent variables) and the arcsine transformation of disturbance intensity (independent variable).

Four lakes in the reference group in 1996 were eliminated from the limnoplankton biomass analyses for the years 1997 and 1998 because these lakes had their watershed logged during the fall of 1996 or winter of 1997. In addition, two reference lakes were not sampled in May 1998. As a result, the sample size for the reference group was 38 in 1996, 34 in 1997, and 32 in 1998 (except for July and September 1998 where n = 34). All analyses were performed on log-transformed values of zooplankton and limnoplankton biomass.

Results

Among-group differences in zooplankton biomass, 1996

There was no detectable difference in the biomass of total zooplankton, cladocerans, and cyclopoids among the three groups of lakes ($p > 0.25$), although burned-watershed lakes had consistently higher biomass than reference lakes (Fig. 1). Calanoid biomass was 43% lower in logged-watershed lakes than in reference lakes (p = 0.01) (Fig. 1). Among-group variation in rotifer biomass was not significant (p = 0.09), although burned-watershed lakes supported 74% more rotifer biomass than reference or logged-watershed lakes (Fig. 1).

Among-group differences in limnoplankton biomass, 1996–1998

During the first year following watershed disturbances (1996), the biomass of the rotifer size fraction of limnoplankton was 59% higher in burned-watershed lakes than in reference lakes (p = 0.03) (Fig. 2D). There were no significant variations in the other size fractions among groups of lakes 1 year after disturbances, although the burned group consistently tended to support greater biomass of limnoplankton than reference lakes, especially for the crustacean size fraction (+41%) (Fig. 2B) and the algal size fraction (+23%) (Fig. 2E).

This tendency for burned-watershed lakes to support higher limnoplankton biomass than reference lakes was even more pronounced 2 years following watershed disturbances (Fig. 2): percent increases ranged from 91% for the rotifer size fraction (p = 0.02) (Fig. 2D) to 65% for the crustacean size fraction (p = 0.08) (Fig. 2B). Increases in the other size fractions of limnoplankton were less than 30% and nonsignificant ($p > 0.45$) (Fig. 2). As a result of these increases in each size fraction in 1997, total biomass of limnoplankton was 50% greater in burned-watershed lakes than in the reference lakes (p = 0.08) (Fig. 2A).

The logged group of lakes supported levels of limnoplankton within ±25% of those of the reference group during the 3 years of the study. Differences were never significant. During the third year following watershed disturbances,

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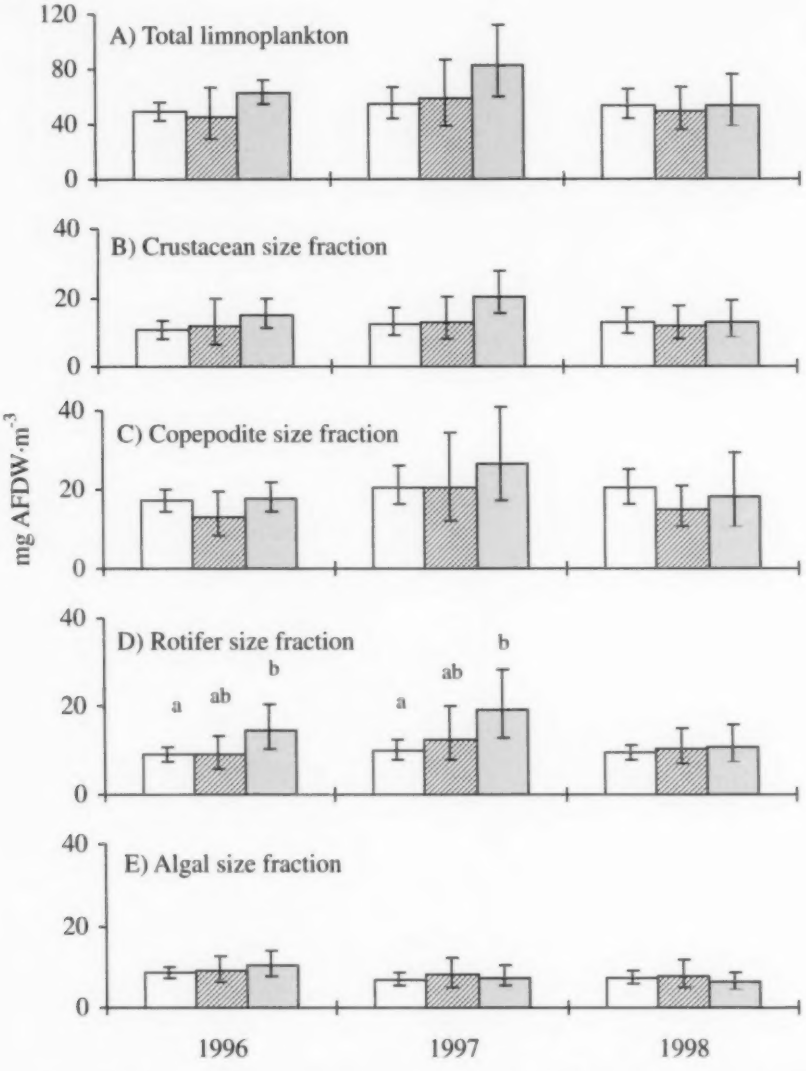
Fig. 2. Among-group differences in total limnoplankton and the four size fractions during the years 1996, 1997, and 1998. Bars represent undisturbed- (open), logged- (hatched), and burned-watershed lakes (shaded). Error bars represent the 95% confidence intervals on the mean (back-calculated from log-transformed values). Bars with different letters represent groups with significantly different means (α = 5%, Scheffé's multiple range test).



limnoplankton biomass levels for all size fractions in the logged and burned groups were within ±25% of those of the reference group of lakes ($p > 0.3$).

The observed among-group differences in mean biomass levels of total zooplankton and total limnoplankton relative to the reference group were generally within ±50% (Figs. 1 and 2A). In contrast, the confidence intervals on the means of each group were large (Figs. 1 and 2A). As a result, the null hypothesis of no effect of watershed condition on total zooplankton and total limnoplankton biomass levels was accepted (Table 2). If, however, the observed heterogeneity among groups of lakes did constitute a true effect of watershed condition, the present study design would have a high probability of not detecting it. This is reflected in the high risks of type II error (Table 2). The same can be said for all other zooplankton variables for which the null hypothesis of no effect was accepted (Table 2). Hence, in the cases where the null hypothesis was accepted, we cannot conclude, with great certainty, that watershed condition does not impact on zooplankton biomass. The size of such an effect, however, would be smaller than a 50% difference with the reference group of lakes.

Sampling period constituted a source of variation in zooplankton biomass severalfold greater than watershed condition (Table 3). We therefore proceeded to analyse among-group variations for each of the three sampling periods sepa-

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Table 2. Power analysis of the F tests conducted on zooplankton biomass in three groups of lakes: undisturbed, logged, and burned catchments.

Variable	Year	Null hypothesis	Type I error probability	Type II error probability
Total zooplankton	1996	Accepted		0.75
Cladocerans	1996	Accepted		0.84
Calanoids	1996	Rejected	0.01	
Cyclopoids	1996	Accepted		0.83
Rotifers	1996	Accepted		0.54
Total limnoplankton	1996	Accepted		0.54
	1997	Accepted		0.41
	1998	Accepted		0.92
Crustacean size fraction of limnoplankton	1996	Accepted		0.74
	1997	Accepted		0.56
	1998	Accepted		0.95
Copepodite size fraction of limnoplankton	1996	Accepted		0.64
	1997	Accepted		0.84
	1998	Accepted		0.79
Rotifer size fraction of limnoplankton	1996	Rejected	0.03	
	1997	Rejected	0.02	
	1998	Accepted		0.83
Algal size fraction of limnoplankton	1996	Accepted		0.79
	1997	Accepted		0.92
	1998	Accepted		0.85

Note: For each test, the probability associated with type I error is indicated if the null hypothesis of no among-group differences was rejected or the approximate probability of type II error if the null hypothesis was accepted.

Table 3. Relative importance of watershed condition and sampling period as factors accounting for variation in zooplankton and limnoplankton biomass.

Variable	Year	F value for watershed condition	p value for watershed condition	F value for sampling period	p value for sampling period
Total zooplankton	1996	1.37	0.27	13.8	0.0001
Cladocerans	1996	0.60	0.56	2.7	0.0776
Calanoids	1996	4.83	0.01	6.6	0.0024
Cyclopoids	1996	0.70	0.51	10.3	0.0001
Rotifers	1996	2.58	0.09	35.5	0.0001
Total limnoplankton	1996	2.35	0.11	25.3	0.0001
	1997	2.77	0.08	83.4	0.0001
	1998	0.17	0.85	11.7	0.0001
Crustacean size fraction of limnoplankton	1996	1.27	0.29	11.7	0.0001
	1997	2.69	0.08	53.2	0.0001
	1998	0.06	0.94	7.4	0.0014
Copepodite size fraction of limnoplankton	1996	1.97	0.15	3.9	0.0255
	1997	0.78	0.47	33.0	0.0001
	1998	1.03	0.37	10.3	0.0001
Rotifer size fraction of limnoplankton	1996	4.02	0.03	25.1	0.0001
	1997	4.78	0.02	36.1	0.0001
	1998	0.40	0.68	2.8	0.0708
Algal size fraction of limnoplankton	1996	0.92	0.41	38.8	0.0001
	1997	0.26	0.78	14.6	0.0001
	1998	0.59	0.56	9.2	0.0003

Note: F values and associated probabilities are indicated for each source of variation. Watershed condition was the main effect factor, while sampling period was a nested factor. For the main effect factor, degrees of freedom for the F values were 2 in the numerator (v_1) and varied with year in the denominator (v_2 = 35 in 1996, 31 in 1997, and 29 in 1998). For the nested factor, v_1 = 2 and v_2 = 70 in 1996, 62 in 1997, and 58 in 1998.

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Table 4. Analysis of variance of zooplankton and limnoplankton biomass by sampling period.

Variable	Year	Sampling period	Mean zooplankton biomass			F	p
			Reference	Logged	Burned		
Total zooplankton (mg dry weight·m^{-3})	1996	June	59	40	63	1.22	
		July	32	34	37	0.15	
		September	23	18	30	1.10	
Cladocerans (mg dry weight·m^{-3})		June	17	15	21	0.15	
		July	10	17	11	0.49	
		September	5	8	13	0.94	
Calanoids (mg dry weight·m^{-3})		June	11	6	7	3.02	0.06
		July	8	5	7	1.45	
		September	6	3	5	2.73	0.08
Cyclopoids (mg dry weight·m^{-3})		June	12	10	17	1.67	
		July	6	5	8	1.11	
		September	3	2	3	0.18	
Rotifers (mg dry weight·m^{-3})		June	4.4	3.1	9.0	3.13	0.06
		July	1.5	1.8	2.4	1.12	
		September	1.1	1.2	1.7	0.88	
Total limnoplankton (mg AFDW·m^{-3})	1996	June	66	54	85	2.00	
		July	49	55	70	1.82	
		September	36	30	42	1.09	
	1997	June	68	64	111	2.25	
		July	75 *a*	101 *ab*	132 *b*	6.44	0.005
		September	32	31	38	0.45	
	1998	June	74	64	75	0.18	
		July	36	37	44	1.14	
		September	62	51	47	0.68	
Crustacean size fraction (mg AFDW·m^{-3})	1996	June	14	16	21	0.79	
		July	11	14	17	1.20	
		September	7	7	9	0.25	
	1997	June	16	21	36	2.43	
		July	18 *a*	23 *ab*	39 *b*	4.70	0.02
		September	6	4	6	0.58	
	1998	June	20	17	23	0.24	
		July	8	10	10	0.62	
		September	14	10	10	0.54	
Copepodite size fraction (mg AFDW·m^{-3})	1996	June	20	14	22	2.33	
		July	16	14	18	0.60	
		September	15	11	14	1.00	
	1997	June	20	20	30	1.02	
		July	33	35	40	0.34	
		September	13	12	15	0.33	
	1998	June	25	23	24	0.04	
		July	13	10	14	1.09	
		September	25	15	17	1.63	
Rotifer size fraction (mg AFDW·m^{-3})	1996	June	14 *ab*	11 *a*	23 *b*	3.93	0.03
		July	9	12	15	1.62	
		September	6	6	9	2.15	
	1997	June	17	13	26	2.38	
		July	10 *a*	24 *b*	29 *c*	7.12	0.002
		September	6	6	9	1.74	
	1998	June	13	12	11	0.10	
		July	7 *a*	8 *ab*	12 *b*	4.24	0.02
		September	11	11	10	0.08	
Algal size fraction (mg AFDW·m^{-3})	1996	June	14	12	14	0.48	
		July	9	12	12	1.43	
		September	5	5	6	1.11	
	1997	June	9	8	11	1.61	
		July	8	11	7	1.30	

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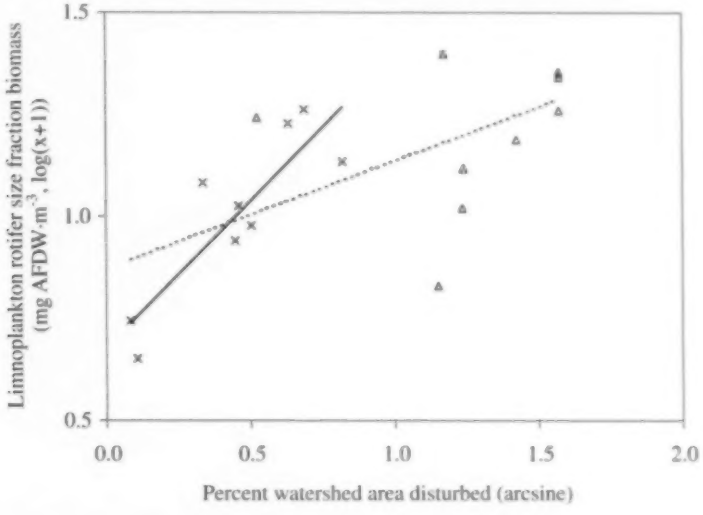
Table 4 (*concluded*).

Variable	Year	Sampling period	Mean zooplankton biomass			F	p
			Reference	Logged	Burned		
Algal size fraction (mg AFDW·m^{-3})	1997	September	5	6	5	0.31	
	1998	June	10	10	8	0.50	
		July	7	7	6	0.12	
		September	6	6	5	0.77	

Note: Mean biomass values for each watershed treatment type (reference, logged, and burned) were back-calculated from logarithms. Degrees of freedom for the F values were 2 in the numerator (v_1) and varied with year in the denominator (v_2 = 35 in 1996, 31 in 1997 and July and September 1998, and 29 in June 1998). Only probabilities (p) of less than 0.1 are indicated. When F values are significant ($p < 0.05$), the results of a Scheffé multiple comparison of means are indicated by a lowercase letter. Means annotated with a single letter (e.g., *a*) are significantly different from other means annotated with a different single letter (e.g., *b*). Means annotated with multiple letters (e.g., *ab*) are not significantly different from either of the named groups.

Fig. 3. Relationship between the biomass of the rotifer size fraction of limnoplankton (dependent variable Y) and disturbance intensity (independent variable X) 1 year after disturbances (1996). Logged-watershed lakes are represented by crosses and burned-watershed lakes by triangles. Regression equation for both types of lakes (broken line): $Y = 0.26X + 0.87$, $n = 18$, $r^2 = 40\%$, $p = 0.005$; regression equation for logged-watershed lakes (solid line): $Y = 0.73X + 0.68$, $n = 9$, $r^2 = 77\%$, $p = 0.002$.



rately. Significant among-group differences were detected during the June or July sampling periods but not during the September sampling period (Table 4). Biomass was generally highest in June and lowest in September. Results of analyses based on each sampling period (Table 4) were consistent with those based on the entire ice-free season (Table 3): among-group variations that were significant for the entire ice-free season were also significant for individual sampling periods. In only one case did analyses by month reveal significant among-group variations not detected by the repeated measure analyses: the rotifer size fraction of limnoplankton in July 1998 was 71% higher in burned-watershed lakes than in reference lakes (Table 4).

The biomass of the rotifer size fraction of limnoplankton in logged- and burned-watershed lakes 1 year after disturbance was positively related to disturbance intensity (Fig. 3). The relationship for both logged- and burned-watershed lakes could be described by a single regression equation. There was, however, practically no overlap in the ranges of disturbance intensity between the logged and burned groups of lakes. Because extrapolating beyond the range of observations for each of the two groups of lakes is untenable, regression analyses were performed for each set of lakes separately (Fig. 3). For the logged group of lakes, 77% of the variation in the biomass of the rotifer size fraction could be explained by disturbance intensity ($p = 0.002$). Similar relationships were observed for the algal size fraction ($r^2 = 71\%$, $p = 0.004$), the copepodite size fraction ($r^2 = 60\%$, $p = 0.01$), and total limnoplankton ($r^2 = 62\%$, $p = 0.01$) but not for the crustacean size fraction of limnoplankton or for any of the taxonomic groups of zooplankton. The range of disturbance intensity in the burned group of lakes was too narrow for any significant relationship to emerge.

Discussion

Our hypothesis of greater zooplankton biomass in disturbed-watershed lakes was supported in the case of burned-watershed-lakes but not in the case of logged-watershed lakes. These biomass increases in burned-watershed lakes relative to reference lakes are consistent with the greater TP, TN, and Chl *a* concentrations observed in the burned group

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of lakes and the positive relationships reported between zooplankton biomass and TP and TN (Yan 1986) and Chl *a* (Pace 1986) in North American lakes. Greater biomass in burned-watershed lakes was most pronounced for the rotifer size fraction of limnoplankton. Rotifers and, more generally, the smaller components of plankton are known to relate more closely to nutrient or Chl *a* concentrations than the larger components of plankton in eastern Canadian oligomesotrophic lakes (Currie et al. 1999). It is interesting to note that although limnoplankton size fractions are composed of many different organisms (cf. Materials and methods), there was good agreement between the results of among-group differences in the rotifer size fraction of limnoplankton and the rotifer taxonomic group 1 year following disturbances.

While the biomass of the smaller rotifer size fraction of zooplankton was higher in burned-watershed lakes during the first and second years following disturbance, the biomass of the larger crustacean size fraction was higher only during the second year. This could reflect the shorter generation time of rotifers relative to crustaceans (Allan and Goulden 1980), allowing rotifers to exploit the available resources before the crustaceans. Crustaceans, in contrast, can demonstrate time lags in response to increases in nutrient concentrations (Smith 1969). Alternatively, the greater biomass of the crustacean size fraction in burned-watershed lakes relative to reference lakes observed during the second year could be the result of a lower predation pressure in the burned group of lakes (Brooks and Dodson 1965). There was some indication that the relative density of small yellow perch (<74 mm) and small lake whitefish (*Coregonus clupeaformis*) (<119 mm) was reduced in logged- and burned-watershed lakes (Magnan and St-Onge 1999), supporting the idea of decreased predation pressure on zooplankton in burned-watershed lakes. Planktivorous fish, however, included more than 10 different species, the total density of which showed no differences among the three groups of lakes. The relative importance of nutrient concentration and fish density in relation to zooplankton biomass remains unclear. With respect to the greater biomass of the rotifer size fraction observed in burned-watershed lakes relative to reference lakes during the first and second year after disturbance, it could, hypothetically, result in a decrease in the efficiency of carbon transfer from algae to fish (Stockner and Shortreed 1989). These authors have argued that rotifers can constitute an energy sink by adding to the number of trophic levels through which matter must flow before reaching fish. The importance of such a phenomenon remains to be quantified.

Contrary to our expectations, there was a general tendency (calanoids excepted) for logged-watershed lakes to support zooplankton biomass equivalent to, or slightly lower than, that of reference lakes. This may in part reflect the lower disturbance intensity in logged- than in burned-watershed lakes. Forestry practices removed on average 38% of forest cover in the logged group, while natural forest fires removed more than 90% in eight out of nine cases. In addition, Québec provincial legislations require that a 20-m buffer strip zone of unharvested vegetation be left along lakes and streams. The lower degree of disturbance in logged-watershed lakes compared with burned-watershed lakes and the buffer strips might have mitigated the nutrient inputs to logged-watershed lakes, thus in part accounting for the absence of detectable zooplankton biomass differences between logged-watershed and reference lakes (with the exception of calanoids). The smaller difference between logged-watershed and reference lakes than between burned-watershed and reference lakes was not only observed for zooplankton biomass but also for algal biomass and Chl *a* concentration (Planas et al. 2000) and TP and TN concentrations (Carignan et al. 2000).

Calanoid biomass was clearly lower in logged-watershed lakes than in reference lakes (–43%, $p = 0.01$). Calanoids are often associated with nutrient-poor environments (Patalas 1972; Pace 1986). In our study, calanoid biomass across the 38 lakes was negatively correlated with TN ($r = -0.40$, $p = 0.01$) and Chl *a* ($r = -0.33$, $p = 0.05$). This suggests that calanoids did better in the nutrient-poor environments of reference lakes than in the richer logged-watershed lakes. The biomass of cyclopoids, rotifers, and the copepodite size fraction of limnoplankton, however, was also lower in logged-watershed lakes compared with reference lakes, although differences were not significant. Lower biomass in logged-watershed lakes was also reflected in total zooplankton biomass and total limnoplankton biomass 1 year after logging. Logged-watershed lakes would therefore seem to support lower zooplankton biomass despite higher TP, TN, and Chl *a* concentrations. DOC concentrations in logged-watershed lakes were higher than in reference or burned-watershed lakes, and as a result, light penetration was reduced by 40% compared with reference lakes (Carignan et al. 1999). We suggest that logged-watershed lakes tend to support lower zooplankton biomass than reference lakes despite higher TP and TN concentrations through light limitation of primary productivity.

Among-group differences in the 1998 limnoplankton biomass were weaker than during the first 2 years following watershed disturbances. The same applies to other environmental variables, for example, the concentrations of nitrate, potassium, sulphate, chloride, and Chl *a* (Carignan et al. 2000; Planas et al. 2000). Natural regeneration of vegetation on the disturbed watersheds may have contributed to curb phosphorus and nitrogen washout and thereby temper the among-group differences in the biomass of primary producers and zooplankton. Alternatively, nutrient inputs from burned watersheds could have remained high in 1998, with, nonetheless, no appreciable among-group differences in limnoplankton biomass. Such a hypothetical scenario could be achieved through increased turnover rates of primary producers, grazers, and planktivorous fish.

Month-to-month variability in limnoplankton biomass among groups of lakes may be related to temporal variability in runoff and element load to lakes. Significant among-group differences in limnoplankton biomass usually occurred in the spring and summer periods (June and July sampling periods) rather than during the fall period (September sampling period). The greater response of limnoplankton biomass to watershed disturbances earlier in the year may be related to greater runoff occurring during this period. For the region under study, between 30 and 40% of annual runoff, and presumably element loss from the watershed, occurs during the months of April and May (roughly corresponding to snowmelt). In contrast, less than 14% of annual runoff usually

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occurs during the months of August and September (S. Lamontagne, Université de Montréal, Montréal Qué., personal communication). Thus, if used as an indicator of watershed disturbance in Shield lakes, limnoplankton should be sampled during the spring and summer periods, when the interactions between the terrestrial and aquatic components of the landscape are greatest.

The present study did not allow us to compare zooplankton biomass between logged- and burned-watershed lakes sharing similar disturbance intensities. The zooplankton biomass differences observed between logged- and burned-watershed lakes can thus be attributed either to a difference in the nature of the disturbance (logging or fire) or to a difference in the intensity of the disturbance or both. There is good evidence that logging and burning have different effects on the chemistry of water, irrespective of disturbance intensity (Carignan et al. 2000). Whether equivalent zooplankton biomass would have been obtained in logged- and burned-watershed lakes with comparable disturbance intensities is a matter of speculation. The positive relationships observed between the biomass of the algal, rotifer, and copepodite size fractions of limnoplankton and disturbance intensity suggest that we could have observed higher biomass in the logged group of lakes than in reference lakes, had the logging covered a greater proportion of watersheds. High percentages of logged-watershed area were seldom achieved, however, in part because the watershed areas were large enough for extensive proportions of them to support unsuitable timber material. Alternatively, it is possible that, with higher percentages of the watershed area logged, the expected increase in plankton biomass would be counteracted by lower light penetration due to increased concentrations of DOC, as already mentioned above.

The biomass values reported in this study were similar to those reported in Yan (1986) for 16 undisturbed Ontario lakes with comparable lake areas and TP concentrations. He presented crustacean biomass values varying from 34 to 103 mg dry weight·m^{-3}, a range comparable with that of 20–163 mg dry weight·m^{-3} observed in our set of 20 reference lakes (sum of cladocerans, calanoids, and cyclopoids). Although no study has previously reported on the comparative effects of logging and forest fires on zooplankton biomass, Rask et al. (1998) did report on cladoceran and copepod densities in one reference lake and three Finnish lakes with 15–33% of the watershed clear-cut. They observed slight increases in the density of cladocerans and copepods in some of the lakes following watershed logging. They did not, however, comment on the magnitude of these increases in comparison with interannual, intermonth, or interlake variability. Their data suggest that these sources of variation were difficult to separate from that associated with watershed disturbance.

With a sample size of 20 reference lakes, nine logged-watershed lakes, and nine burned-watershed lakes, the present study was powerful enough to detect significant among-group variations in the following cases: calanoid biomass 1 year following disturbances was 43% lower in logged-watershed lakes than in reference lakes and rotifer size fraction biomass of limnoplankton 1 and 2 years following disturbances was at least 60% greater in burned-watershed lakes than in reference lakes. The among-group variations in the other taxonomic groups and size fractions were generally smaller than 50% and statistical power was too low to detect potential differences (at $\alpha = 5\%$). Because logging activities rarely affect 90% of a watershed's area like wildfires do, and because regulations require that a 20-m buffer strip be left between logged areas and water resources, both types of disturbances could not be compared on the basis of equal disturbance intensities. Nonetheless, as they occur in reality, logging activities and forest fires seem to have opposite impacts on the biomass of zooplankton of eastern Canadian Boreal Shield lakes. Wildfires seem to be associated with greater zooplankton biomass than reference lakes, especially the smaller, rotifer size fraction of limnoplankton. On the contrary, logging activities seem to be associated with decreases in zooplankton biomass, especially calanoids, in comparison with reference lakes.

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Impact of logging and natural fires on fish communities of Laurentian Shield lakes

Isabelle St-Onge and Pierre Magnan

Abstract: The goal of this study was to determine if natural fires and logging have a significant impact on abundance, growth, and size structure of fish populations in 38 lakes of the Laurentian Shield (Québec, Canada). The watersheds of nine of these lakes underwent logging and nine underwent natural fires, while the 20 remaining lakes were used as references. No significant differences were found among the three lake groups in the catch per unit of effort of the most abundant species: white sucker (*Catostomus commersoni*), northern pike (*Esox lucius*), yellow perch (*Perca flavescens*), lake whitefish (*Coregonus clupeaformis*), fallfish (*Semotilus corporalis*), brook trout (*Salvelinus fontinalis*), walleye (*Stizostedion vitreum*), and burbot (*Lota lota*). No significant difference was found among control, burned, and logged lakes in the back-calculated length of yellow perch, for which age determinations were made. However, we found that the proportions of small yellow perch and white sucker were significantly lower in populations of impacted lakes (burned and logged lakes pooled). The influence of logging and fires remained significant when a series of biotic and abiotic variables on watershed and lake characteristics were accounted for in multiple regression analyses. The lower proportion of small fish in impacted lakes could be due to an increase in postemergence mortality or to a shift of individuals to the pelagic zone.

Résumé : Le but de cette étude était de déterminer si les coupes forestières et les feux de forêt ont un impact significatif sur l'abondance, la croissance et la structure en taille des populations de poissons de 38 lacs du bouclier laurentien (Québec, Canada). Les bassins versants de neuf lacs ont fait l'objet de coupes forestières, ceux de neuf autres ont subi des feux de forêt, alors que les 20 restants ont été utilisés comme référence. Aucune différence significative n'a été observée entre les trois groupes de lacs au niveau des captures par unité d'effort des espèces les plus abondantes : le meunier noir (*Catostomus commersoni*), le grand brochet (*Esox lucius*), la perchaude (*Perca flavescens*), le grand corégone (*Coregonus clupeaformis*), la ouitouche (*Semotilus corporalis*), l'omble de fontaine (*Salvelinus fontinalis*), le doré jaune (*Stizostedion vitreum*) et la lotte (*Lota lota*). Aucune différence significative n'a été observée dans les longueurs rétrocalculées des perchaudes, pour lesquelles la détermination d'âge a été effectuée, entre les lacs témoins, brûlés et coupés. Cependant, une diminution significative de la proportion des individus de petite taille a été observée chez les populations de perchaudes et de meuniers noirs des lacs perturbés (les lacs brûlés et coupés formant un seul groupe). L'influence des coupes et des feux est demeurée significative après que les variables biotiques et abiotiques caractérisant les bassins versants et les lacs ont été considérées dans des analyses de régression multiple. La plus faible proportion des individus de petite taille dans les lacs ayant subi des perturbations pourrait être due à une augmentation de la mortalité post-émergence ou à un déplacement des individus dans la zone pélagique.

Introduction

The effects of logging are well documented in lotic ecosystems (reviewed in Roberge 1996). Some of the most significant effects are the increase in stream flow (Van Der Vinne and Andres 1988*b*; Heede 1991), nutrient concentrations (Nicolson et al. 1982; Plamondon et al. 1982), and turbidity and sedimentation (Krause 1982; Everest et al. 1987). Road construction and road use associated with logging are often more significant causes of increased sediment yield than logging itself (Van Der Vinne and Andres 1988*a*; Miller et al. 1997). Logging may also induce increases in water temperature (Beschta et al. 1987; Garman and Moring 1991), decreases in dissolved oxygen (Ringler and Hall 1975; Murphy and Milner 1997), and increases in primary productivity (Murphy and Hall 1981; Gregory et al. 1987) resulting from canopy removal. Forest fires have also been reported to increase sediment transport (Beaty 1994; Cerdà et al. 1995) and nutrient losses (Spencer and Hauer 1991; Bayley et al. 1992). In lakes, forest removal, either through natural fires or logging, also tends to increase organic carbon, chlorophyll *a*, and limnoplankton biomass (Carignan et al. 2000; Patoine et al. 2000; Planas at al. 2000).

All these changes may impact the top-down and bottom-up trophic interactions, including fish populations, which can reflect short-term changes in limnetic eutrophication due to their ability for rapid growth compensation and their short life history cycles. As fish yield is strongly correlated with lake productivity, forest clearance may increase fish produc-

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tivity (Roberge 1996). Increased sedimentation following deforestation is also likely to have an impact on spawning habitats and therefore on fish recruitment (Everest et al. 1987). Most studies on the impact of logging on fish populations deal with salmonids inhabiting running waters. With the exception of Bérubé and Lévesque (1998), we do not know of any study that investigated the impact of these perturbations on fish population structure of lake ecosystems. Two studies of this issue deal with the potential effect of deforestation on salmonid lake habitats (Gunn and Sein 2000; Steedman and Kuskneriuk 2000).

The objective of our study was to determine if abundance, growth, and size structure of fish populations are correlated with changes in any lake characteristics following wildfires or logging.

Methods

Study area

The data were collected in 38 stratified headwater lakes on the Laurentian Shield, located within a 50 000-km^2 area around Réservoir Gouin, Québec (for a detailed description of the study area, see Carignan et al. 2000). Our study compared fish communities in lakes with three types of watershed treatments: 20 control lakes with undisturbed watershed, nine "logged" lakes, whose watersheds had undergone forest clearance (8.5–73.2%), and nine "burned" lakes, whose watersheds had been severely burned by fire (50.1–100.0%). Lakes were selected on the basis of comparable size, depth, watershed morphometrics, and time of impact (see Carignan et al. 2000). Most fires and clearcuts occurred in 1995 (with the exception of Lakes C24 and C2, which had partial cuts in spring and summer 1994, respectively). The fish communities of these lakes are generally unexploited or lightly exploited due to the relatively limited access.

Fish sampling

Twenty-one lakes were sampled in 1996 (1 year after impact) and 17 in 1997 (2 years after impact). Each lake was sampled once between June and August. Fish were captured with experimental monofilament gill nets, 102.3 m long × 2.7 m deep, with stretched mesh panels of 20, 24, 33, 36, 50, 60, 76, 90, and 100 mm (filament diameter of 0.17, 0.20, 0.20, 0.20, 0.20, 0.32, 0.32, 0.32, and 0.32 mm, respectively). Gill nets were set perpendicular to the shore, with small and large meshes alternating from the shore among gill nets. The nets were set at regular intervals around the lake, the first net location being randomly located on aerial photographs. The fishing effort was six nets per night for lakes <50 ha, eight nets per night for lakes of 50–100 ha, 10 nets per night for lakes of 100–150 ha, and 12 nets per night for lakes >150 ha. The nets fished for periods of 16–24 h, covering the periods between 18:00 and 09:00. For all fish captured, total length (±1 mm) and weight (±0.1 g) were noted and, when possible, sex was determined by gonad examination. Appropriate bone structures were also removed for further age determination of white sucker, northern pike, yellow perch, brook trout, lake whitefish, and walleye.

Study species

The fish species composition of the study lakes, unknown before the study, was quite diverse (Table 1). The most widespread species were white sucker (31 lakes), northern pike (27 lakes), yellow perch (25 lakes), and lake whitefish (11 lakes). We selected white sucker, yellow perch, and lake whitefish to evaluate the impact of logging or fires on fish population structure because they were the most abundant and frequent species. Northern pike was present in many lakes, but its abundance (catch per unit of effort (CPUE), number of fish per gill net per night) was too low to build reliable length distributions (mean CPUE: 2.1 ± 1.3, n = 27 lakes).

Relative abundance

Lakes where few individuals were captured (i.e., <15 per species) were not included in the analyses. A one-way analysis of variance (ANOVA) followed by Tukey's multiple range comparison test was performed to determine if there were any significant differences in CPUE among lake groups for species for which sufficient data were available to perform this analysis (e.g., white sucker, northern pike, yellow perch, and lake whitefish). Assuming that logging and fires may have similar effects on abundance (if there is an effect), we pooled the data from logged and burned lakes into a single group, hereafter referred as impacted lakes, to increase sample size of the other species (e.g., fallfish, brook trout, walleye, and burbot). In this case, we used a t test to compare control versus impacted lakes. When the data were not normally distributed and (or) the variances heterogenous, the data were $\log(x + 1)$ transformed. The homogeneity of variances was tested with the F_{max} test (Sokal and Rohlf 1981), while normality was tested with the Kolmogorov–Smirnov–Lilliefors test. The data were not always normally distributed and (or) the variances homogeneous after transformation. We assumed that departures from these assumptions had no marked effect on the t test or ANOVA significance levels (Sokal and Rolf 1981).

We also compared the percent CPUE of "small fish" of the three study species and that of age-1+ yellow perch using the same procedure because they appeared to be affected by logging and fires (see Fig. 1 and below for age determination of yellow perch). Small fish corresponded to the first mode of the size frequency distribution, which was estimated visually. In the size frequency distribution, the frequency of each length-class represented the mean of the lake group. For yellow perch, the first mode was clear and corresponded to fish <75 mm in length (see Results section). For white sucker, the first mode was not as clear as for yellow perch but was set to include fish <160 mm. Finally, the first size-class of lake whitefish comprised fish <120 mm.

Age and growth of yellow perch

Opercular bones were used to determine age and growth of yellow perch. Pairs of operculars were placed in a solution of soapy water overnight and then cleaned and dried. A dissecting microscope connected to an image analyser was used for the examination of operculars. The bone structure was submerged in immersion oil and observed at 6.5–10× magnification on a black background with a continuous light ring. An image of the bone was then captured with Sigma Scan Pro® (version 4.0) and viewed on a monitor. The true annuli were characterized by a gradual change from the broad opaque summer growth zone to a narrow transparent winter zone, which ends relatively abruptly with a sharp line of discontinuity to the next summer zone (LeCren 1947). This line was taken as the end of the year's growth. Two independent readings were made by the same reader. When the results differed, two additional readings were made; when there was still disagreement, the sample was rejected. The opercular centrum was considered to be the point in the thickest region of the bone where the holes appeared to converge (LeCren 1947). A straight line was then traced perpendicularly between the centrum and the edge of opercula, corresponding to the opercular length. The opercular length as well as successive annual growth increments were measured to the nearest 0.01 mm with the image analyser.

We back-calculated body lengths at previous ages following two proportional back-calculation methods: the scale-proportional hypothesis (SPH) and the body-proportional hypothesis (BPH). A detailed description of these methods can be found in Francis (1990).

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Table 1. Occurrence of fish species in the three groups of sampled lakes (control, logged, and burned).

Species	Control	Logged	Burned	Total
White sucker (*Catostomus commersoni*)	18	6	7	31
Northern pike (*Esox lucius*)	13	7	7	27
Yellow perch (*Perca flavescens*)	12	7	6	25
Lake whitefish (*Coregonus clupeaformis*)	4	3	4	11
Fallfish (*Semotilus corporalis*)	4	4	2	10
Brook trout (*Salvelinus fontinalis*)	4	2	1	7
Walleye (*Stizostedion vitreum*)	4	2	3	9
Burbot (*Lota lota*)	3	3	1	7
Lake trout (*Salvelinus namaycush*)	0	1	1	2
Rainbow smelt (*Osmerus mordax*)	2	0	0	2
Trout-perch (*Percopsis omiscomaycus*)	1	0	0	1
Brook stickleback (*Culaea inconstans*)	1	0	0	1
Ninespine stickleback (*Pungitus pungitus*)	1	0	0	1
Finescale dace (*Phoxinus neogaeus*)	4	1	0	5
Lake chub (*Couesius plumbeus*)	3	2	0	5
Golden shiner (*Notemigonus crysoleucas*)	1	3	1	5
Pearl dace (*Margariscus margarita*)	4	0	3	7
Blacknose shiner (*Notropis heterolepis*)	0	1	0	1
Spottail shiner (*Notropis hudsonius*)	2	0	0	2
Logperch (*Percina caprodes*)	0	0	1	1
Northern redbelly dace (*Phoxinus eos*)	2	0	0	2
Common shiner (*Luxilus cornutus*)	1	0	0	1
Cyprinid sp.	14	1	8	23

Note: Values indicate the number of lakes that each taxa inhabited per category.

In 80% of lakes, the R^2 of the body length–scale length relationships was above 0.95. For this reason, neither back-calculation method was preferred (BPH versus SPH) because no substantial differences were found in back-calculated fish lengths (Pierce et al. 1996). In this paper, we present the results computed with the SPH method. We used back-calculated length-at-age to compare growth among the three lake groups (control, burned, and logged). To reduce the interannual variability, comparisons were made only among fish of the same cohort and of the same lag preceding or following the impact (e.g., age-1 fish 1 year after logging). Since all fish sampling was not done in the same year, this approach allowed us to use 2 years of data in the same analyses (see Results section). This procedure was carried out on the first three cohorts (ages 1–3) for a total of 5 back-calculated years: the 2 years both preceding and following the impacts as well as for the year of the impacts. A one-way ANOVA followed by Tukey's multiple range comparison test was performed for each year in each cohort to determine if there were any significant differences in fish length among lake groups. Finally, we used a t test to compare control and impacted lakes (pooled data from logged and burned lakes).

Multiple regressions

Stepwise multiple linear regressions (forward selection) were used to build models with each of the following dependent variables: percent 1-year-old yellow perch in the population and percent of white sucker <160 mm in the population. No model was built to predict the relative abundance of small lake whitefish in the population because of the low sample size (nine lakes). Watershed and lake morphometry, water quality, phytoplankton, and zooplankton were used as independent variables in statistical analyses (Table 2). Methodological details concerning estimation of these variables can be found in Carignan et al. (2000), Patoine et al. (2000), and Planas et al. (2000). Water quality, phytoplankton, and zooplankton were sampled three times during the summers of 1996 and 1997. For these variables, we used the mean of the three summer samples in statistical analyses (for the summer when fish were sampled). The variable "logging or fires" was entered as a dummy variable where the value 0 was attributed to control lakes and 1 to those that underwent logging or fires. As fish were not sampled simultaneously in all of the lakes during the summer, we also created a variable "sampling date," which was the day of the year. All variables that were not normally distributed were transformed (log or arcsin transformed for proportion). The number of independent variables used in the procedure was always lower than the number of lakes. In the stepwise procedure, the independent variable that enters on the first step is the most highly correlated with the dependent variable. The best model, as indicated by the highest R^2 values and the lowest values of the mean square error associated with the estimate, was retained. Collinearity between the independent variables was evaluated by examination of the pairwise correlation coefficients. Independent variables that were highly correlated (e.g., r = 0.7–1.0) were not considered simultaneously in regression analyses. The tolerance level given in the Systat regression procedure was also taken into account to prevent collinearity. When collinearity occurred, each collinear variable was used to build a separate model that was then compared with all of the other models. Residual scatterplots, normal probability plots, and partial residual plots were used to determine if the assumptions of the multiple linear regression were satisfied (i.e., normality, linearity, and homoscedasticity of residuals).

Results

Relative abundance

No significant differences were found in CPUE among the three lake groups for white sucker, northern pike, yellow perch, lake whitefish, fallfish, brook trout, walleye, and burbot (Table 3). Similarly, no significant differences were found in CPUE of the most frequent species between control

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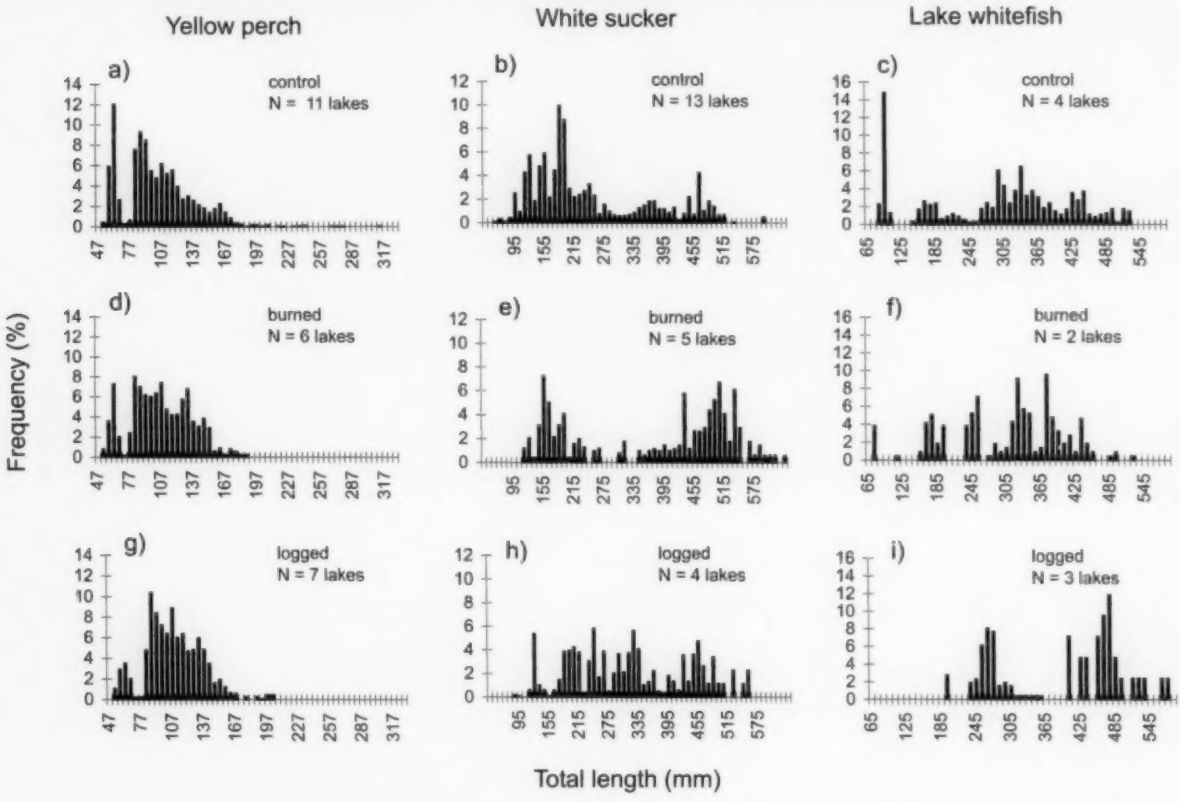
Fig. 1. Length frequency distribution of yellow perch, white sucker, and lake whitefish populations sampled in 1996 or 1997 in control, burned, and logged lakes. For each length-class, frequency represents the mean of the lake group.



and impacted lakes (i.e., when burned and logged lakes were pooled) (Table 3). The mean percent CPUE of small white sucker (<160 mm) in the population was significantly lower in impacted lakes than in control lakes ($t = -2.15$, $p < 0.05$) (Fig. 1). The mean percent CPUE of small yellow perch (<75 mm) and small lake whitefish (<120 mm) also tended to be lower in impacted than in control lakes, but these differences were not significant (Fig. 1). In lakes sampled in 1996, the mean percent CPUE of 1+ yellow perch in the population was significantly lower in logged lakes than in control lakes ($F = 9.913$, $p < 0.05$), with burned lakes showing an intermediate value (Fig. 2*a*). Such a difference in mean percent CPUE among lake groups was not observed in 1997 (Fig. 2*b*). The same pattern was observed for 1+ yellow perch in pooled samples of 1996 and 1997 ($F = 4.289$, $p < 0.05$) (Fig. 2*c*). A significant increase in the mean percent CPUE of 3+ yellow perch was also observed in burned lakes compared with control lakes (pooled years: $F = 6.024$, $p < 0.01$). As the abundance is expressed as percent CPUE, the significant increase in abundance of 3+ yellow perch is probably due to the significant decrease of 1+ individuals.

Growth of yellow perch

No significant differences were found in the back-calculated length of yellow perch among control, burned, and logged lakes (Table 4). No significant differences were observed when logged and burned lakes were pooled into impacted lakes (Table 4).

Determinants of the proportion of 1-year-old yellow perch and small white sucker (<160 mm) in the population

The best predictors of the percent CPUE of 1-year-old yellow perch in the population were the biomass of northern pike (–), mean summer lake temperature (+), the dummy variable logging or fires (–), and depth of the epilimnion (+), explaining 29.4, 24.6, 19.5, and 13.1% of the variation, respectively (Table 5). The length of brooks in the watershed (+) explained 0.5% of the variation (Table 5). The abundance of white sucker and the nanophytoplankton density appeared in the model as suppressor variables (i.e., a regressor that is virtually uncorrelated with the dependent variable but is useful in the model because it accounts for some residual variance in the other independent variables that is irrelevant for the prediction of the dependent variable; Tabachnick and Fidell 1983). Given the presence of these suppressor variables (Table 5), this model explained a total of 81.3% of the variation of percent CPUE of 1-year-old yellow perch in the population.The most powerful predictors of the percent CPUE of small white sucker were the density of

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Table 2. Independent variables available for multiple regression analyses.

Categorie	Variable	Units
Geographical	Latitude	Decimal
	Longitude	Decimal
	Altitude	m
Lake morphology	Lake area	km^2
	Fetch	km
	Lake perimeter	km
	Shoreline development	
	Mean lake slope	%
	Mean littoral slope	%
	Lake volume	m^3
	Epilimnion volume	m^3
	Littoral volume	m^3
	Littoral area	m^2
	Maximum depth	m
	Mean depth	m
	Epilimnion depth	m
Watershed morphology	Watershed area	km^2
	Drainage area	km^2
	Watershed perimeter	km
	Drainage density	$km \cdot km^{-2}$
	Length of brooks on watershed	km
	Runoff	$m^3 \cdot year^{-1}$
	Water residence time	Years
	Mean watershed slope	%
	Marsh on watershed	km^2
Physical and chemical	Secchi depth	m
	Mean lake temperature	°C
	Mean lake oxygen	$mg \cdot L^{-1}$
	Mean epilimnion temperature	°C
	Mean epilimnion oxygen	$mg \cdot L^{-1}$
	Thermocline depth	m
	Dissolved organic carbon	$mg \cdot L^{-1}$
	Total phosphorus	$\mu g \cdot L^{-1}$
	Total nitrogen	$\mu g \cdot L^{-1}$
	Nitrate	$\mu g \cdot L^{-1}$
	pH	
	Alkalinity	$\mu equiv. \cdot L^{-1}$
Phytoplankton	Chlorophyll *a*	$\mu g \cdot L^{-1}$
	Picophytoplankton density	$\mu g \cdot L^{-1}$
	Nanophytoplankton density	$\mu g \cdot L^{-1}$
	Microphytoplankton density	$\mu g \cdot L^{-1}$
Zooplankton	Total volume of particles	$mm^3 \cdot m^{-3}$
	Volume of particles <1000 μm	$mm^3 \cdot m^{-3}$
	Volume of particles >1000 μm	$mm^3 \cdot m^{-3}$
	Ash-free dry weight of particles 50–100, 100–200, 200–500, and >500 μm	$mg \cdot m^{-3}$
Fish	Abundance or biomass of northern pike	$No. \cdot net^{-1}$ or $g \cdot net^{-1}$
	Abundance or biomass of walleye	$No. \cdot net^{-1}$ or $g \cdot net^{-1}$
	Abundance or biomass of white sucker	$No. \cdot net^{-1}$ or $g \cdot net^{-1}$

microphytoplankton (+), the dummy variable logging or fire (–), latitude (+), and sampling date (+), which together accounted for 73.6% of the variation (Table 5).

Discussion

Our study indicates that logging and fires affect the abundance of small yellow perch and white sucker. This is confirmed by the continued presence of the dummy variable logging or fires in the multiple regression models after all others biotic and abiotic variables were accounted for. Furthermore, the variable logging or fires explained a substantial proportion of the variation of 1+ yellow perch (19.5%) and small white sucker (24.1%). When logging and fires

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Table 3. CPUE of fish species in the three lake groups (control, logged, and burned).

Species	Control	Logged	Burned	p_1	p_2
White sucker[a,b]	10.2±12.0 (18)	8.4±9.9 (6)	3.6±2.9 (7)	0.569	0.35
Northern pike[a]	2.0±1.5 (13)	1.9±1.2 (7)	2.6±0.8 (7)	0.3525	0.7096
Yellow perch[a,b]	23.4±35.9 (12)	11.7±9.2 (7)	9.6±4.6 (6)	0.7464	0.4611
Lake whitefish[a,b]	10.3±5.6 (4)	6.4±7.0 (3)	5.5±8.4 (4)	0.3552	0.1239
Fallfish[a]	5.5±6.1 (4)	1.4±0.6 (4)	1.9±2.6 (2)	nt	0.2921
Brook trout[a]	5.5±6.9 (4)	5.8±7.7 (2)	25.8 (1)	nt	0.4599
Walleye[a]	9.4±4.6 (4)	7.1±0.1 (2)	6.9±3.8 (3)	nt	0.4018
Burbot	0.2±0.1 (3)*	0.3±0.1 (3)	0.8 (1)*	nt	0.3331

Note: Data represent mean ± SD; number of lakes is given in parentheses. p_1, probability of ANOVA (among control, logged, and burned); p_2: probability of t test (between control and impacted). *Difference determined by Tukey's test; nt, not tested due to low sample size.

[a]ANOVA performed on log-transformed data.

[b]t test performed on log-transformed data.

were considered separately as independent variables, they did not appear to predict the CPUE of small yellow perch and white sucker in any model. This is probably due to the splitting of samples size (four logged lakes and five burned lakes for white sucker and seven logged lakes and six burned lakes for yellow perch), leading to an increased probability of making a Type II error. In pooling logged and burned lakes, we assumed that both perturbations have similar impacts on small fish.

The impacts of logging are well documented in fish and usually include a decrease in spawning habitat quality. In streams, the increase in temperature and sedimentation after timber harvest can affect egg to fry survival by reducing the oxygen in spawning grounds and by forming physical barriers to emergence (Ringler and Hall 1975; Everest et al. 1987). Forest fires also influence the amount of sediment found in brooks and streams (Beaty 1994; Cerdà et al. 1995). In lakes, the removal of fringing vegetation may also affect spawning habitat quality. For example, fine suspended sediment may be carried around the lake shoreline by water movements and be deposited in spawning grounds (Miller et al. 1997). In some Québec lakes, Bérubé and Lévesque (1998) reported a reduction in sportfishing yield (abundance and biomass) of brook trout after clear-cutting. Possible damage to spawning and nursery habitats was suggested to partially explain these reductions in fishing success.

Most studies on the impact of fires and logging on fish populations have been done on salmonids because they require clean gravel or rubble substrate to spawn, so their reproduction is generally affected by siltation (Berkman and Rabeni 1987). Yellow perch spawn in shallow water of lakes or in tributaries where single, convoluted egg strands are either attached to submerged plants and fallen trees or are deposited on sand and gravel (Scott and Crossman 1973). For this reason, yellow perch are assumed to be less sensitive than trout to the potentially adverse affects of timber harvesting (France 1997); this probably explains why no study has evaluated the impact of logging and fires on this species. In the present study, the reduction in abundance of 1+ yellow perch cannot be attributed to a reduction in egg to fry survival caused by logging or fires. The reduction in abundance was observed in 1996, 1 year after forest harvesting or fires. The 1-year-old yellow perch captured in 1996 were born in spring 1995, before fires and most logging activities occurred. Consequently, any reduction in the abundance of 1+ yellow perch in the littoral zone would have occurred in the seasons following the emergence of larvae.

White sucker require clean gravel to spawn (Scott and Crossman 1973) and thus could have a response to spawning habitat degradation by siltation similar to that of salmonids (Berkman and Rabeni 1987). As we did not do age determinations for white sucker, we cannot evaluate the effect of fires and logging on the first cohort. However, age–length relationships found in the literature suggest that individuals captured in our gill nets were older than 1 year, including fish under 160 mm. The gillnet selectivity against small fish seems to be responsible for the absence of 1-year-old white sucker in all sampled lakes.

Little information is available on postemergence survival after clearcuts and fires. Depending on the concentration and duration of exposure, suspended sediments can induce physiological stress, reduce growth, and cause direct mortality in fish (Newcombe and MacDonald 1991). In streams where watersheds have been almost completely burned, Bozek and Young (1994) found dead fish following storm flow caused by rain. Fish appeared to have been asphyxiated by sediment that completely obstructed their gills. In streams, the current velocity is strong enough to keep sediment in suspension and thus expose fish to a substantial stress. In contrast, lake basins act as sinks (Miller et al. 1997) where sediment is rapidly deposited. Furthermore, adult fish appear to tolerate suspended sediment concentrations substantially greater than those commonly found in nature (Muncy et al. 1979). For these reasons, it is unlikely that an excess of suspended sediments would have caused direct mortality of fish in burned and logged lakes, especially in logged lakes, due to presence of buffer strips.

Assuming that fine sediment can reach the shores of burned and logged lakes, macroinvertebrate habitats and survival could have been negatively affected, reducing the abundance of food for yellow perch and white sucker. Some reviews have reported a reduction in macroinvertebrate density or diversity following timber harvesting (Gregory et al. 1987; Hartman and Scrivener 1990). Thus, a lower food availability or quality could have influenced the survival of younger fish.

Some studies have reported an increase in salmonid biomass or growth despite a decrease in reproductive habitat

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Fig. 2. Age frequency distribution of yellow perch in control, burned, and logged lakes sampled in (*a*) 1996, (*b*) 1997, (*c*) 1996 and 1997 (pooled samples). For each age-class, frequency represents the mean of the lake group.

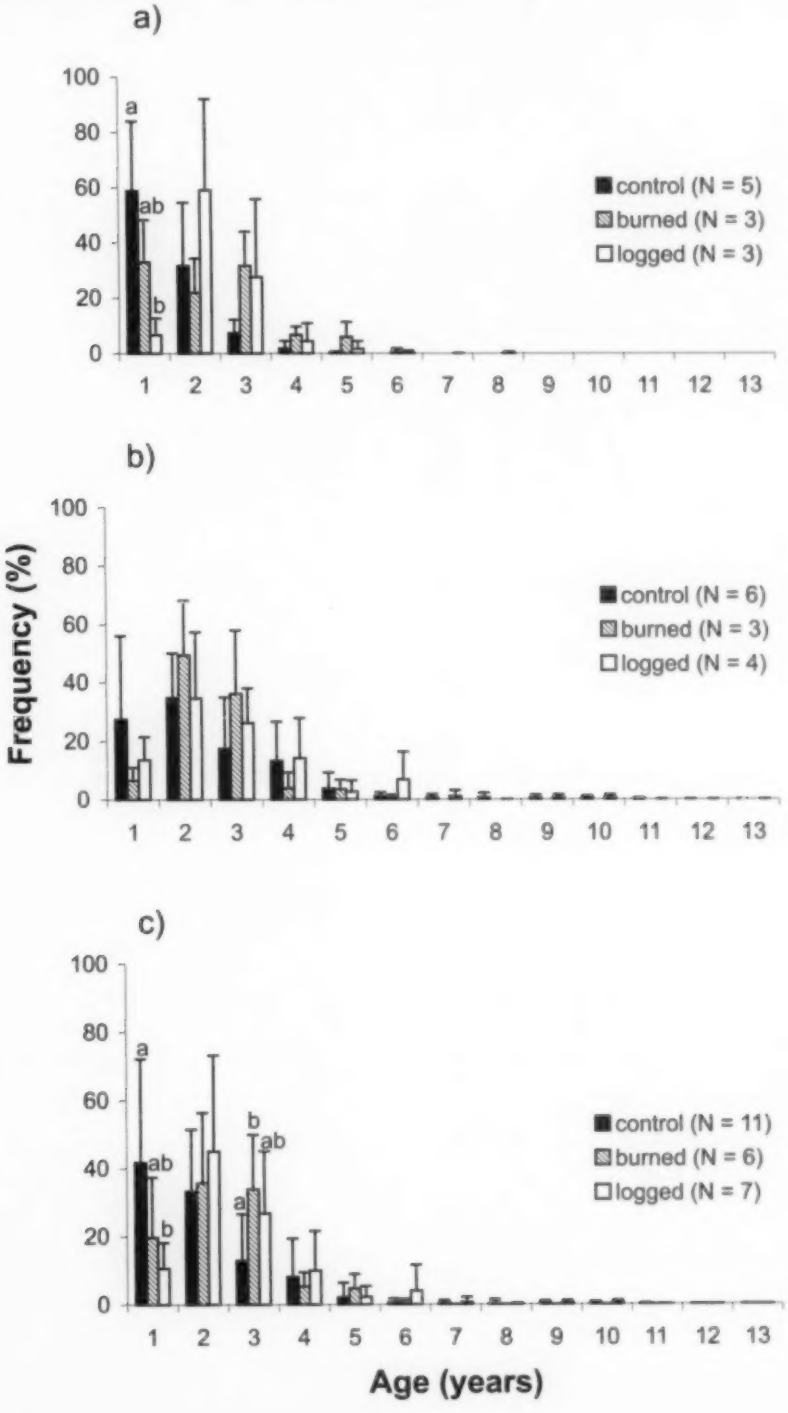

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Table 4. Back-calculated length of yellow perch 2 years before, the year of, and 2 years after fire and logging impacts.

		2 years before perturbations			1 year before perturbations			Year of perturbations			1 year after perturbations			2 years after perturbations		
Age group	Lake group	Mean	SD	*N*	Mean	SD	*N*	Mean	SD	*N*	Mean	SD	*N*	Mean	SD	*N*
I	Control	48.02	7.41	7	49.18	6.05	9	48.58	8.73	11	52.45	5.23	11	51.16	5.87	6
	Burned	44.46	4.04	5	47.46	10.44	5	49.14	3.45	6	48.02	4.13	6	46.41	4.84	3
	Logged	47.17	4.49	4	47.61	6.34	6	49.89	3.75	7	51.00	3.88	6	50.24	2.95	4
	ANOVA	ns	ns		ns	ns		ns	ns		ns	ns		ns	ns	
	t test	ns	ns		ns	ns		ns	ns		ns	ns		ns	ns	
II	Control	80.37	8.53	5	76.98	11.70	7	79.49	5.74	10	82.48	5.05	11	81.34	5.15	6
	Burned	68.92	7.67	3	70.65	5.49	5	75.34	6.43	5	80.67	7.93	6	79.17	2.84	3
	Logged	81.67	8.61	3	73.32	3.92	4	75.55	7.34	6	81.48	6.69	7	83.30	6.22	4
	ANOVA	ns	ns		ns	ns		ns	ns		ns	ns		ns	ns	
	t test	ns	ns		ns	ns		ns	ns		ns	ns		ns	ns	
III	Control	104.06	24.02	2	104.16	14.57	5	101.92	11.45	7	111.93	13.14	10	109.97	9.84	6
	Burned	102.87	—	1	92.95	13.27	3	94.84	7.27	5	102.37	8.70	5	116.02	14.09	3
	Logged	96.29	—	1	106.47	11.31	3	93.57	3.64	4	102.21	5.87	6	112.75	10.40	4
	ANOVA	ns	ns		ns	ns		ns	ns		ns	ns		ns	ns	
	t test	ns	ns		ns	ns		ns	ns		$p < 0.05$	ns		ns	ns	

Note: Statistical analyses were done on separate treatment levels (ANOVA) and in pooling fires and logged lakes into a single group (*t* test); ns, not significant.

Table 5. Best models predicting the percentage of 1-year-old yellow perch and small white sucker (<160 mm) in the population.

Model	$p > t$	SE	R^2 (%)	Adjusted R^2 (%)	SE_{xy} (%)
% of 1-year-old yellow perch in population =			81.3	73.1	16.6
–2.11	0.0067	0.6766			
–0.18 northern pike biomass[a]	0.0012	0.0505	29.4		
+1.67 mean summer lake temperature[a]	0.0006	0.3899	24.6		
–0.25 logging or fires[b]	0.0142	0.1046	19.5		
+0.15 depth of epilimnion	0.0102	0.1371	13.1		
+0.23 length of brooks in watershed[a]	0.0457	0.0898	0.5		
+0.36 nanophytoplankton density[a,c]	0.0184	0.1144	(–0.02)		
–0.34 white sucker abundance[a,c]	0.0094	0.0448	(–5.8)		
% of white sucker of length <160 mm in population =			80.2	74	14.5
–20.21	0.0004	4.5602			
+0.66 microphytoplankton density[a]	0.0000	0.1113	30.7		
–0.31 logging or fires[b]	0.0002	0.0645	24.1		
+0.40 latitude	0.0006	0.0928	10.0		
+0.01 sampling date	0.0017	0.0017	8.8		
–0.21 littoral area[a]	0.0728	0.1113	6.7		

quality (Murphy and Hall 1981; Grant et al. 1986). These authors suggested that the loss of reproductive habitat was compensated for by an increase in primary productivity following disturbance. In our study, the increased phosphorus supply in burned lakes caused a significant (80%) upsurge in biological productivity, as evidenced by higher planktonic and attached chlorophyll levels, algal biomass, and zooplankton (Carignan et al. 2000; Patoine et al. 2000; Planas et al. 2000). In contrast, the increased total phosphorus levels in logged lakes did not result in higher productivity, either because higher concentrations of dissolved organic carbon reduced light availability or because of differences in biological availability of phosphorus released by burned and harvested watersheds (Carignan et al. 2000). As no difference was found in its growth, yellow perch did not respond to the increased productivity in burned lakes.

The gill nets used in this study were chosen to ensure the capture of all species and of a large size range of fish. However, these nets are not efficient in capturing small fish like 1-year-old yellow perch and small white sucker. It is possible that an increase in the catchability of small fish occurred as the summer progressed and the fish grew larger. This could explain the selection of the variable sampling date (+) in the model explaining the percentage of small white sucker in the population (Table 5). The absence of such a relationship in the yellow perch model could be due to specific differences in catchability. The possible increase in catchability of small fish as the summer progressed could explain the

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lower abundance of small yellow perch and white sucker in impacted lakes only if these lakes had been systematically sampled at the beginning of the summer and control lakes at the end, which was not the case. Our sampling effort was evenly distributed among treatments through 1996 and 1997. Furthermore, the impact of logging and fires remained significant when sampling date was accounted for in multiple regression analyses. Nevertheless, a detailed estimation of small size-class structure of fish in these lakes would need a more targeted sampling strategy (e.g., smaller mesh size, seine, trawl, or traps). It is also possible that small yellow perch and white sucker move to the pelagic zone following littoral zone disturbances of logged and burned lakes (e.g., following a reduction in macroinvertebrates discussed above); this zone was not sampled with our protocol.

In the model predicting the proportion of small white sucker, the density of microphytoplankton explained a large proportion of the variation, suggesting that this fish is influenced by lake productivity. The biomass of northern pike was the most important determinant of the abundance of small yellow perch. Northern pike is a common predator of yellow perch (Scott and Crossman 1973); a preliminary examination of northern pike stomach contents from this study revealed that small yellow perch were frequently eaten. Mean summer lake temperature and epilimnion depth were also good predictors of the proportion of 1+ yellow perch in the population, probably because they are both related to yellow perch habitat. It is known that growth and survival of perch larvae are positively correlated with temperature (e.g., Guma'a 1978; Wang and Eckmann 1994). The epilimnion depth reflects the availability of habitat selected by young yellow perch; the use of upper waters by juveniles is probably due to temperature requirements for growth (Becker 1983), foraging (Bergman 1987), and (or) avoidance of large piscivores (Werner 1986).

In conclusion, this study suggests that logging and fires have an impact on small yellow perch, white sucker, and perhaps lake whitefish, either through an increase in post-emergence mortality or to a shift of individuals to the pelagic zone. If this is the case, these mortalities may have a cascading effect on the most valuable exploited species like northern pike and walleye, which use yellow perch, white sucker, and lake whitefish as forage fish. We do not know of any study that has investigated the impact of these perturbations in lake ecosystems with such a large sample size and on nonsalmonid species. Our sampling design allowed us to observe significant differences in population structure among lake treatments but not to determine the mechanisms responsible for these patterns. Further studies will be needed to investigate the function of fish populations following forest removal by clear-cutting or burning.

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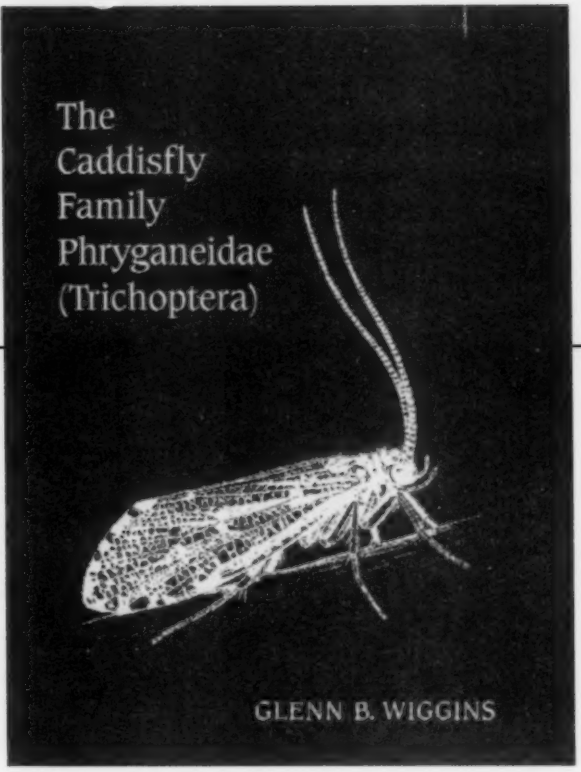

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